THE ANATOMY AND PHYLOGENETIC RELATIONSHIPS OF *ANTETONITRUS INGENIPES* (SAUROPODIFORMES, DINOSAURIA): IMPLICATIONS FOR THE ORIGINS OF SAUROPODA

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DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

(Signature of candidate)

18th day of January 2013 in Wits

ABSTRACT

A thorough description and cladistic analysis of the *Antetonitrus ingenipes* type material sheds further light on the stepwise acquisition of sauropodan traits just prior to the Triassic/Jurassic boundary. Although the forelimb of *Antetonitrus* and other closely related sauropododomorph taxa retains the plesiomorphic morphology typical of a mobile grasping structure, the changes in the weight-bearing dynamics of both the musculature and the architecture of the hindlimb document the progressive shift towards a sauropodan form of graviportal locomotion. Nonetheless, the presence of hypertrophied muscle attachment sites in *Antetonitrus* suggests the retention of an intermediary form of facultative bipedality. The term Sauropodiformes is adopted here and given a novel definition intended to capture those transitional sauropodomorph taxa occupying a contiguous position on the pectinate line towards Sauropoda. The early record of sauropod diversification and evolution is re-examined in light of the paraphyletic consensus that has emerged regarding the 'Prosauropoda' in recent years.

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION AND LITERATURE REVIEW

1.1 GENERAL INTRODUCTION

Sauropoda, "undoubtedly the most spectacular" (Chatterjee and Zheng 2002:145) of all the dinosaur groups, has furnished paleontological science with literature now spanning three centuries and over 120 valid genera (Upchurch et al. 2004; Remes 2008). The late 20th and early 21st centuries, especially, saw an exponential increase in the study of sauropod dinosaurs, with a general consensus emerging in regards to the evolutionary relationships of late Jurassic and Cretaceous sauropods (Upchurch 1995,1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004). Furthermore, there is now little doubt that the morphological complex that so easily distinguishes sauropods as unique among dinosaur groups – the long neck, massive size and columnar limbs – was well established by the Early Jurassic (e.g., Cooper 1984; He et al. 1998; Bandyopadhyay et al. 2010), and several important finds within the last two decades suggest a late Triassic origin for the clade (Buffetaut et al. 2000; Yates and Kitching 2003; Bonnan and Yates 2007; Ezcurra and Apaldetti 2012). In addition to yielding significant insight towards our understanding of the anatomy of the earliest sauropods, these finds have also contributed to a growing consensus that the traditional 'prosauropod' assemblage represents a paraphyletic grade of basal forms with respect to Sauropoda (Yates and Kitching 2003; Pol 2004; Yates 2007a,b, 2010; Upchurch et al. 2007b; Smith and Pol 2007; Ezcurra 2010; Pol et al. 2011; Novas et al. 2011; Ezcurra and Apeldetti 2012). It is a view that has prompted a re-evaluation of the patterning and timing of the evolutionary changes within Sauropodomorpha at the Triassic-Jurassic boundary.

However, although it is now generally appreciated that the evolutionary history of Sauropoda extends much earlier than previously recognised, the exact nature of the transition from Sauropodomorpha to Sauropoda remains poorly understood. This confusion is exacerbated by an early sauropod record in which only fragmentary forms are known from rocks earlier than the Toarcian, as well the instability of several derived

sauropodomorph taxa within a number of recent cladistical analyses (e.g., Upchurch et al. 2007; Pol et al. 2011, Apaldetti et al. 2012).

The large sauropodomorphs from the Lower Elliot Formation of South Africa (Norian/Rhaetian, Upper Triassic), with their unique combination of plesiomorphic and apomorphic traits, represent a significant addition to the sauropodomorph record, and a means of better unravelling the origins of the sauropod bauplan (Yates and Kitching 2003; Yates 2007a,b; Bonnan and Yates 2007; Pol and Powell 2007). One species in particular, *Antetonitrus ingenipes*, displays a unique combination of primitive and derived traits and is therefore ideally positioned – both temporally and morphologically – to inform on the acquisition of a number of distinctive sauropod adaptations (Yates and Kitching 2003). When Yates and Kitching (2003:1755) first described and named *Antetonitrus ingenipes* they stated that it "represents an important mid-point between more gracile basal sauropodomorphs with an inferred facultative bipedal gait and the specialised graviportal obligate quadrupedality of later eusauropods".

This intermediate morphology helps eliminate a stratigraphic gap of some 20 million years in which the sauropod bauplan was previously observed to appear suddenly at the outset of the Jurassic (Sereno 1999; Wilson 2002; Wilson and Sereno 1998), and several recent topologies have recognised *Antetonitrus* as one of the basal-most sauropods known (Yates 2007a,b; Allain and Aquesbi 2008; Pol et al. 2011; Apaldetti et al. 2011). However, this position was based only on preliminary descriptive data, and a thorough comparative analysis of the *Antetonitrus* assemblage – both in terms of its phylogenetic relationships and functional morphology – remains to be undertaken. As our understanding of the stepwise acquisition of traits that led to Sauropoda remains poorly delineated, this study aims to address the continued gaps in our knowledge of early sauropod evolution by providing a thorough description and comparative analysis of the type material of *Antetonitrus*.

1.2 THE ELLIOT FORMATION OF SOUTH AFRICA

The Elliot Formation is an Upper Triassic ('Lower' Elliot Formation) to Lower Jurassic ('Upper' Elliot Formation) fluvio-lacustrine succession that skirts the western side of the Lesotho/Free State border before terminating at its thickest point (300m) near Jamestown in the Eastern Cape (**Fig. 1**). Together with the underlying Molteno and overlying Clarens formations, it forms part of the stratigraphic Stormberg Group and represents the final depositional stages of the Karoo Supergroup – a large foreland basin to the north of the Cape Fold Belt (Catuneanu et al. 1998; Bordy et al. 2004, 2005).

Work (both stratigraphic and biostratigraphic) within the Elliot formation has been sporadic over the past century, with various authors traditionally placing the lower part of the "Triassic Red Beds" as either Carnian (e.g. Gauffre 1993; Galton and van Heerden 1998; Anderson et al. 1998; Warren and Damiani 1999) or Norian (Cooper 1984; Knoll 2004) in age. Kitching and Raath (1984) proposed a subdivision of the Elliot Formation into three bio-zones (Lower, Middle, Upper) based on the association of certain faunal assemblages with changes in lithostratigraphy. Subsequent reviews of the biostratigraphy of the Elliot formation have broadly agreed with Kitching and Raath's faunal interpretation, with Lucas and Hancox (2001) ultimately proposing that the assemblage of large 'prosauropods', cynodonts, rauisuchians and ichnofossils from lower part of the formation best correlated with Norian deposits elsewhere in the world (e.g. the Los Colorados formation of Argentina). They also stated that because the massospondylids, tritylodontids, and sphenosuchians of the upper deposits clearly depicted an early Jurassic assemblage, a date any older than the Norian for the lowermost Elliot was unlikely as it would infer an improbably long hiatus between the upper and lower members (Lucas and Hancox 2001:7). However, a lack of absolute dates precludes a reliable constraint on the temporal boundaries of the formation.

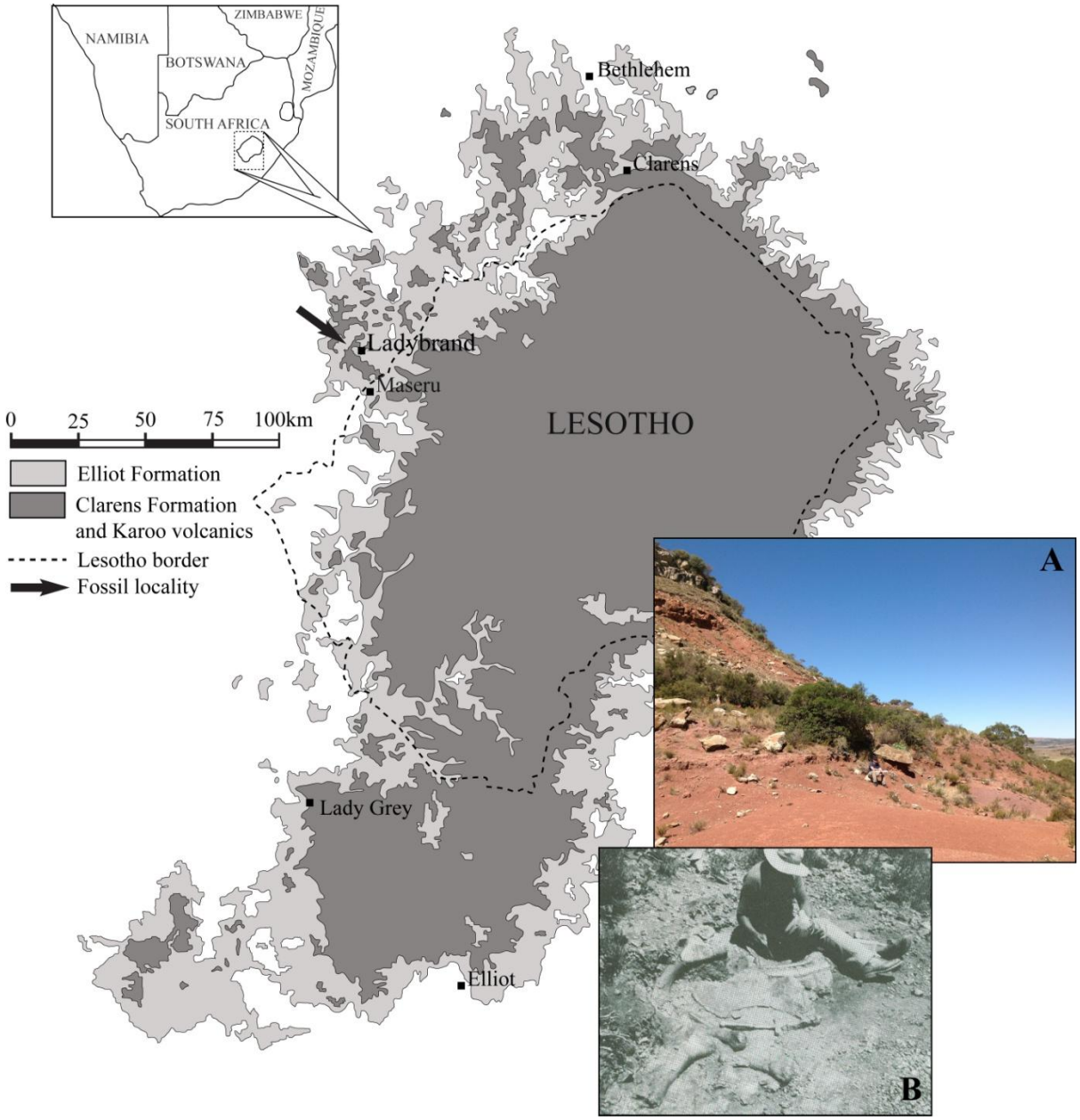

Fig. 1. The Elliot Formation of South Africa showing the type locality of the *Antetonitrus ingenipes* fossil assemblage (modified from Bordy et al. 2004). **A**, the author seated at the base of the saddle where *A.ingenipes* was discovered. **B**, the original excavation of *A.ingenipes* (from Kitching and Raath 1984).

More recently, the interpretation of Lucas and Hancox (2001) was corroborated and further refined over a series of intensive investigations into the depositional history of the Elliot Formation by Bordy et al. (2004a,b; 2005; 2006). Citing a marked textural contrast between the Lower and Upper Elliot Formation, Bordy et al. (2004:399) formalised a new arrangement in which Kitching and Raath's "Middle" unit was subsumed into the Upper

unit; the reorganised Lower and Upper Elliot Formation therefore correlating with the *Euskelosaurus* and *Massospondylus* Range Zones of Kitching and Raath (1984), respectively. Although the taxonomic validity of *Euskelosaurus* will be discussed further below, this stratigraphic arrangement continues the long-established observation that the lower part of the formation is dominated by a late Triassic assemblage of large sauropodomorphs, whereas the early Jurassic Upper Elliot Formation (UEF) is better known for producing abundant remains of the smaller, gracile 'prosauropod' *Massospondylus*. The work of Bordy et al. (2005) was also significant for its interpretation of the Molteno-Elliot contact as an abrupt unconformity (as opposed to the lower Elliot being the distal, coeval equivalent of the Molteno, as previously had been suggested [Cole 1992; Anderson et al. 1998]). Furthermore, this unconformity is thought to be related to a minor loading event in the Cape Fold Belt, the end of which has been dated at 215 ± 3 Ma (Halbichet al. 1983). This would suggest that the earliest occurrence of the Lower Elliot Formation (LEF) is comfortably within the Norian at about 215 million years ago.

Geomorphologically, the substantially thicker LEF is characterized by channel-shaped sandstone bodies a few tens of meters wide and a maximum of 20 to 25 meters high that are separated by thicker (20-30m) and laterally persistent mudstone intervals (Bordy et al. 2004). It is within these mudstone units that the majority of fossil material is found. The depositional environment of the LEF is generally characterised as one of perennial meandering river systems with extensive floodplains and overbank areas, evincing a humid to semi-arid climate dominated by riparian forests and inhabited by large bodied animals (Bordy et al. 2004, 2005, 2006). There appears to have been a depositional hiatus of perhaps as many as 5+ million years between the LEF and the UEF due to the final orogenic loading of the Cape Fold Belt. During this time the area embodied by the Elliot Formation became elevated and erosion took place, coupled with sporadic episodes of pedogenic development (as demonstrated by the common presence of paleosols and calcareous concretions at the boundary between the two units). Once sedimentation resumed during the UEF it was at a slower pace in a progressively more arid environment that has been characterised as an ephemeral fluvial system of small braided streams over an abandoned floodplain (Bordy et al. 2004, 2006).

It is on account of this shift in paleoenvironmental conditions that the LEF is believed to have supported animals of a considerably larger size-class than the relatively smaller massospondylids and sphenosuchian archosaurs of the UEF. Hence, the LEF, with its early age and megafaunal assemblage, is of greatest interest to researchers studying the origins of Sauropoda and the dramatic increase in size that accompanied their development. Although the dinosaurian diversity of the UEF has risen in recent years, especially with the discovery and description of the moderately large 'prosauropod' *Aardonyx celeste* (Yates et al. 2010; see also Yates et al. 2011), most of the animals exceeding 8-10 meters in size are exclusive to the LEF. This is once more evident in light of the new discovery of the partial remains of an as-yet undescribed sauropodomorph (BPI/1/5339/7129) – "the Highland Giant" – that is another magnitude of size larger than *Antetonitrus ingenipes* (although it is possible that it represents an adult of similar taxonomic affinity).

1.2.1 SAUROPODOMORPHA AND THE LOWER ELLIOT FORMATION

There are five valid sauropodomorph taxa currently recognized from the Lower Elliot Formation (Yates 2004b). This follows a period of intensive lumping in which many of the sauropodomorph species (e.g. *Euskelosaurus browni*, *Euskelosaurus africanus*, *Orinosaurus capensis*, *Gigantoscelis molengraaffi*, *Eucnemesaurus fortis*, *Plateosauravus stormbergensis*, *P. cullingworthi*, *Melanorosaurus readi*) named during the early years of South African paleontology (usually based on rather poorly preserved material, see Haughton 1924) were ultimately moved into the ubiquitous 'waste-basket' taxon of *Euskelasaurus browni* Huxley 1866 by Van Heerden in 1979.

However, investigation into the 'enigma' of *Euskelosaurus* by Yates and Kitching (2003) and Yates (2003b, 2004b, 2007a,b) over the past decade has convincingly shown *E. browni sensu* Van Heerden (1979) to be a *nomen dubium* on account of the lack of diagnostic character traits in the type specimen. Furthermore, the hypodigm of *E.browni* is polytypic due to a profusion of conflicting character data – the result of a quarter century's worth of ascribing every large sauropodomorph that was found within the LEF to *E.browni*. Reorganising the

assemblage of LEF sauropodomorphs within a framework of diagnostic morphological attributes, Yates (2003b, 2004b, 2007a,b) currently indentifies the following diagnostic taxa:

PLATEOSAURAVUS Huene 1932

P. cullingworthi Huene 1932

(=*Plateosaurus cullingworthi* Haughton 1924)

(=*Euskelosaurus browni* Van Heerden 1979)

Syntype: SAM 3341–3356, 3602–3603, 3607–3609; Haughton 1924; van Heerden 1979; Yates 2003b)

Diagnosis: Yates (2003b, 2007a) has suggested that *Plateosauravus* can be diagnosed by an unusual combination of characters not found in any other basal sauropodomorph. These include (quoting largely from Yates 2003b:63): posterior dorsal neural spines reaching a height that is more than twice the length of their base; a relatively slender humerus where the width of the distal end is less than one third of the total humeral length; a strongly sinuous deltopectoral crest that is only 42% of the total humeral length (both these humeral traits appear superficially derived); postacetabular process of the illium is square-ended and the ischial peduncle has a posterior 'heel'; femur of moderately large size (at least 545mm) that is sinuous in both lateral and anterior views; fourth trochanter is located entirely in the proximal half of the posterior surface, well away from the medial edge; the descending posterolateral process of the distal tibia extends laterally as far as the anterolateral process; and the presence of a bevelled embayment above the descending posterolateral process of the distal tibia.

Comments: *Plateosauravus cullingworthi* captures a substantial amount of material that had previously been referred to *Euskelosaurus browni* by Van Heerden (1979) (see Yates 2003b), however, a formal diagnosis and comprehensive description of the material collected under *Plateosauravus* awaits publication. Although regularly recovered as a particularly basal taxon (i.e. non-plateosaurian) in recent analyses, future investigation may lead to a re-evaluation of its phylogenetic position. Recent fieldwork within the LEF has unearthed more relatively well preserved *Plateosauravus* material, but this is still awaiting proper description (Yates, pers. comm.).

EUCNEMESAURUS van Hoepen 1920

E.fortis van Hoepen 1920

(=*Euskelosaurus browni* Huene 1906)

(=*Aliwalia rex* Galton 1985)

Holotype: TM 119

Referred material: (NMW 1889-XV-39, 1876-VII-B124, BP/1/6107, 6110 – 6115, 6220; Yates 2007a)

Diagnosis (Yates 2007a): The femur represents the most diagnostic element and is distinct from other sauropodomorphs in displaying an elongate femoral head; a large posterior tubercle on the posterior surface of the femoral head that represents a curious reversal to the non-dinosaurian condition (the only other dinosaur to share it being PVL 3805, an Argentinean specimen generally grouped within *Riojasaurus*); a pronounced lesser trochanter that is higher than wide with an abrupt proximal termination; and a medio-distally curving fourth trochanter with a profile that is rounded rather than the subrectangular shape seen in most basal sauropodomorphs. *E. fortis* has also recently been shown (Yates et al. 2012) to be in possession of a potentially pneumatic subfossa that excavates the wall of the posterior infradiapophyseal fossa on the posterior dorsal vertebra of BP/1/6107.

Comments: Based on a single peculiar femur, this poorly known taxon was, until recently, thought to represent the 'herrerasaurid' dinosaur *Aliwalia rex* (Galton 1985; Paul 1988). However, the discovery of a similarly diagnostic femur found in association with sauropodomorph vertebrae led Yates (2007a) to resurrect the long forgotten *Eucnemesaurus fortis* Van Hoepen 1920 as this taxon represented the first time an '*Aliwalia*-type' femur had been found and ascribed a name that evoked neither a carnivorous basal saurischian nor the problematic *Euskelosaurus* (of which it was also once considered synonymous [Heune 1906; Cooper 1980]). Although based on exceedingly fragmentary material, *Eucnemesaurus* has been consistently recovered as the sister taxon to *Riojasaurus* within a monophyletic Riojasauridae in most recent phylogenetic analyses (e.g., Yates et al. 2007a,b; Apaldetti et al. 2011, 2012). A partially articulated sauropodomorph skeleton

possibly representing a specimen of *Eucnemesaurus* (BP/1/6234) was unearthed in the Eastern Cape in 2003. However, this also is awaiting formal description and diagnosis.

MELANOROSAURUS Haughton 1924

M.readi Haughton 1924

Lectotype: to be established (Nair pers. comm).

Referred specimens: SAM-PK-K3449, SAM-PK-K 3450, NM QR1551, NM QR3314; Galton et al. 2005; Yates 2007b; Bonnan and Yates 2007).

Diagnosis: (Yates 2003b; Galton et al. 2005; Yates 2007a,b; Bonnan and Yates 2007). This species can be distinguished from other basal sauropodomorphs by: tall dorsal neural spines (at least 1.5 times as long as high) dorsoventrally deep hyposphenes (equal to the diameter of the neural canal) on the dorsal vertebrae; proximal caudal vertebrae with median ventral fossae; the presence of at least four sacral vertebrae; a relatively deep radial fossa on the proximal ulna; a femur that is straight in anterior view and semi-elliptical in cross section; a crest-like lesser trochanter that is shifted laterally; and a fourth trochanter with the proximal end lying on the medial margin of the femoral shaft. *Melanorosaurus* has also recently been shown to display the following cranial autopomorphies (Yates 2007b): a transversely broad internarial bar; and enlarged premaxilla; a short ridge on the dorsolateral surface of the posterior end of the maxilla; loss of the anterovental process of the nasal; an elongate vomer; an anterposteriorly shortened fossa on the posterior ventral margin of the basiparasphenoid plate and a broad, dorsoventrally shallow anterior neural canal.

Comments: *Melanorosaurus* is perhaps the most well known sauropodomorph within the LEF. It is often considered (given that many of the above-listed characters are relatively advanced for a basal sauropodomorph) to reside close to the base of Sauropoda, and may even represent the immediate sister taxon to Sauropoda (e.g. Upchurch et al. 2007b; Yates 2007a,b, 2010). *Melanorosaurus* was originally based on a composite collection of postcranial bones (SAM-PK-K3449, 3450), and later had the partial remains of two individuals (catalogued as NM QR1551) also referred to it (Galton et al. 2005). However, in 1994 a group of researchers from the National Museum, Bloemfontein found a largely complete and

articulated skeleton (NM QR3314) with a complete skull while undertaking fieldwork in the Ladybrand District, Free State. This individual was finally subjected to a systematic analysis and description by Yates (2007b) and Bonnan and Yates (2007). The *Melanorosaurus* hypodigm is currently under revision by Jay Nair from the University of Queensland.

BLIKANASAURUS Galton and van Heerden 1985

B.cromptoni Galton and van Heerden 1985

Holotype: SAM K403

Referred material: (BP/1/5271a; Yates 2008)

Diagnosis (Galton and van Heerden 1985, 1998; Yates 2003b, 2008): A curiously robust (given its small size) sauropodomorph that can be distinguished from other sauropodomophs in the Lower Elliot Formation via a smoothly rounded posteromedial margin of the astragalus in dorsal view; a shortened third metatarsal (40% of the length of the tibia); and a first metatarsal in which the midshaft width is 55% of the total length, with a markedly thick distal articular surface in which the dorsoventral depth is 70% of the transverse width (Yates 2008).

Comments: This poorly known species is based primarily on a left epipodium, tarsus and pes (SAM K403), with only a first metatarsal (BP/1/5271a) having been additionally referred to it (Yates 2008). Galton and Van Heerden (1985:511) originally described *Blikanasaurus* as "an early experiment in the direction of heavily-built quadrupedal saurischians, but it was not on the evolutionary line that gave rise to the Sauropoda." This interpretation was based on the marked robustness of the remains and the fact that the distal tarsals are displaced medially, yet the fifth metatarsal is small and undeveloped – as in 'prosauropods'. However, recent phylogenetic assessments suggest a close relationship between Blikanasaurus and Sauropoda (Yates and Kitching 2003; Yates 2007b). The remains, while remarkably stocky, also indicate a curiously small individual.

Blikanasaurus is also of interest as the holotype was found at the very bottom of the southern section of the LEF where it meets the underlying Molteno Formation (Charig et al.

1965). The occurrence of another specimen (BP/1/5271a) in the upper 20m of the LEF and located in the attenuated northern third of the basin (where it overlies the Kaapval Crayton), indicates that the northern section of the LEF probably represents a condensed deposit that is coeval and biostratigraphically homogenous with the thicker southern section (Yates 2008). This seemingly early appearance of sauropod-like forms has interesting implications for the radiation and diversification of basal sauropodomorphs in the upper Triassic of this part of Gondwanaland.

ANTETONITRUS Yates and Kitching 2003

A.ingenipes Yates and Kitching 2003

This form has been recovered as a very basal sauropod in a number of recent phylogenies (e.g., Yates 2007a,b; Allain and Aquesbi 2008; Pol et al. 2011). Excavated by Kitching in 1982, it was originally informally ascribed to *Euskelosaurus browni* (Kitching and Raath 1984). It was later recognised by Yates as belonging to a wholly different taxon and described accordingly (Yates and Kitching 2003). *Antetonitrus ingenipes* shares many similarities with *Melanorosaurus readi*, and most of its derived characters can be viewed as part of a transformation series that proceeds from the plesiomorphic condition in non-sauropodan sauropodomorphs to the apomorphic condition of Sauropoda. As this species represents the focus of the present study, no further description will be given at this point, and a full diagnosis is given below.

1.2.2 INTERNATIONALLY CONTEMPORANEOUS TAXA AND DEPOSITS

With the exception of North America, sauropodomorphs tend to constitute the most abundant and diverse body fossils in the majority of Late Triassic dinosaur assemblages (Barrett and Upchurch 2005; Irmis 2010, see references therein; Langer et al. 2010a).

The sauropodomorph assemblage of the LEF is perhaps best mirrored by the late Norian Los Colorados Formation of north-western Argentina. As with the LEF, the fluvial sandstones of

the Los Colorados Formation record a humid to sub-humid environment of episodic floodplains populated by a dinosaur assemblage predominantly composed of large-bodied sauropodomorphs (Bonaparte 1972, 1978; Caselli et al. 2001; Arcucci et al. 2004; Ezcurra and Apaldetti 2011). This assemblage includes *Riojasaurus incertus* (Bonaparte 1972): a large, primitive taxon known from several individuals that was traditionally grouped within the 'melanorosaurids', but has been resolved more recently as the sister-taxon of *Eucnemesaurus* within Riojsauridae (e.g., Yates 2007a,b); *Coloradisaurus brevis:* a basal taxon closely related to South Africa's *Massospondylus* that was recently recovered as the sister taxon to *Lufengosaurus* within the monophyletic Massospondylidae (Bonaparte 1978; Apaldetti et al. 2012); and *Lessemsaurus sauropoides*: the most advanced sauropodomorph of the Los Colorados Formation and one that is often resolved as the sister-taxon of *Antetonitrus* (Bonaparte 1999; Pol and Powell 2007). Additionally, the fragmentary remains (PULR 136: a tibia is the only completely preserved bone) of a particularly robust sauropodomorph were described recently by Ezcurra and Apaldetti (2011), further indicating the joint importance of South America and South Africa in documenting the spatial and temporal distribution of 'near-sauropod' taxa at the end of the Triassic.

Sauropodomorph-bearing deposits contemporaneous (Norian-Rhaetian) with the LEF also include the Nam Phong Formation of Thailand (*Isanosaurus*: Buffetaut et al. 2000), the Caturrita Formation of Brazil (*Unaysaurus*: Leal et al. 2004), the Laguna Colorada Formation of Patagonia in the south of Argentina (*Mussaurus*: Pol 2004; Pol and Powell 2007b) and the German Keuper Group (*Plateosaurus; Efraasia*: Yates 2003c; Moser 2003). The fissure-filling deposits and Rhaetian beds of Western Europe have also produced sauropodomorph material (Benton and Spencer 1995; Storrs 1994; Galton 2001). Currently, *Camelotia* from Somerset in England is the sole sauropodomorph from the north of Pangea that shares a similar transitional morphology to those large-bodied forms of the Lower Elliot and Los Colorados formations (Galton 1998). It is thus clear that although sauropodomorphs of both gracile and robust morphology are much better known from the Gondwanan deposits of southern America and Africa, they had nonetheless achieved near-global distribution by the latest Triassic.

1.3 RECENT INTERPRETATIONS OF SAUROPODOMORPH PHYLOGENETICS AND THE DEFINITION OF SAUROPODA

Earlier studies of sauropodomorph systematics were seriously hindered by a scarcity of fossil remains and a lack of general consensus on what constitutes a definitive sauropod. It was partly on account of this lack of evidence that a monophyletic 'Prosauropoda', sister-taxon to a monophyletic Sauropoda, became the consensus view of the seminal works on sauropodomorph systematics (e.g., Cruickshank 1975; Galton 1976, 1990; Upchurch 1995, 1997, 1998; van Heerden 1997; Sereno 1989,1999; Wilson 2002; Galton and Upchurch 2004). This idea was probably best encapsulated by Wilson and Sereno's (1998) oft-cited stem-based definition of Sauropoda as "sauropodomorphs more closely related to *Saltasaurus* than *Plateosaurus".* Implicit in this definition was the understanding that the Late Triassic to Early Jurassic array of smaller, bipedal 'prosauropods' represented a mutually exclusive sister-group to Sauropoda, one that had diverged from an unknown common ancestor sometime in the early Late Triassic. This dichotomous reading of sauropodomorph interrelationships effectively implied a twenty million year 'ghost-lineage' of early sauropod ancestors that had yet to be recognised within the fossil record.

Although this idea found support in early cladistical analyses of 'prosauropod' ingroup relationships (Galton 1990; Sereno 1999; Benton et al. 2000), the phylogenetic analysis of increasingly comprehensive data matrices (both in number of characters and taxa) within the last decade has repeatedly challenged the notion of 'prosauropod' monophyly.

Yates and Kitching (2003) were the first to conduct a cladistical analysis of a fully inclusive Sauropodomorpha ('Prosauropoda' + basal Sauropoda) that incorporated in excess of 200 characters. The taxonomic scope of this study was therefore more inclusive than earlier analyses which were generally limited to 'prosauropod' ingroup relationships (e.g. Galton 1990; Sereno 1999; Benton et al. 2000). Their results represented the first time since Gauthier's (1986) original analysis of saurischian relationships that 'prosauropod' paraphyly was expressed within a cladistic framework. However, in contrast to Gauthier's (1986) analysis, which was still mired in the now long-abandoned assumption that 'prosauropods' separated into "narrow-footed" vs. "broad-footed" groups (Galton 1973, 1976), the analysis

of Yates and Kitching (2003) recovered a topology that has been recreated with varying degrees of refinement in almost every subsequent analysis (e.g., Pol 2004; Yates 2007a,b; Upchurch et al. 2007b; Marteniz 2009; Ezcurra 2010; Pol et al 2011; Apaldetti et al. 2011).

This topology can be broadly characterised as an array of central sauropodomorph taxa (i.e., *Plateosaurus*; *Massospondylus*; *Lufengosaurus*; *Riojasaurus;* sometimes referred to as 'core prosauropods') flanked basally by increasingly distant gracile taxa (i.e., *Efrassia*, *Thecodontosaurus, Pantydraco* and *Saturnalia*) and apically by successively advanced 'sauropod-like' taxa (i.e., *Jingshanosaurs*; *Yunnanosaurus*; *Anchisaurus*; *Melanorosaurus*). The great majority of recent topologies (e.g., Yates 2007a,b, 2010; Yates et al. 2010; Smith and Pol 2007; Pol et al. 2011; Apaldetti et al. 2011) have presented this arrangement as an highly pectinate array of basal sauropodomorphs expressing complete paraphyly with Sauropoda. On the contrary, Upchurch et al. (2007b) recovered a monophyletic 'plateosaurian' clade composed of several taxa traditionally regarded as 'core prosauropods'; an idea further expounded upon by Sereno (2007). Independent of which tree(s) represents the most likely hypothesis of basal sauropodomorph interrelationships, it has become evident that traditional definitions (e.g. Wilson and Sereno 1998; Sereno 1999) expressing the relationship of Sauropoda to its more basal sauropodomorph outgroups are no longer adequate.

In studies where definitions of a fully monophyletic and mutually exclusive 'Prosauropoda' were anchored in *Plateosaurus*, basal Sauropoda consisted of only a few poorly known forms of which *Vulcanodon karabaensis* from the early Jurassic (?Toarcian) of Zimbabwe was the most basal (Salgado et al. 1997). However, given the paraphyletic consensus of prosauropoda that emerged in recent years, the content of Sauropoda as defined by Wilson and Sereno (1998) had consequently expanded to capture a number of basal sauropodomorphs not traditionally regarded as sauropods (e.g., *Massospondylus*; *Jingshanosaurus; Yunnanosaurus; Anchisaurus*). Yates (2007a) therefore proposed Massopoda to designate the clade formed of all sauropodomorphs more closely related to Sauropoda than to *Plateosaurus*, thus inluding Sauropoda as well as the successively basal Anchisauria, Massospondylidae, and Riojasuridae. This definition captures the same taxa as Sauropoda *sensu* Wilson and Sereno (1998), but restricts the latter label to those large, obligatory quadrupedal forms traditionally regarded as sauropods. Yates' nomenclature has

been widely adopted in most recent phylogenetic analyses (Yates 2007a,b; et al. 2010; Smith and Pol 2007; Novas et al. 2011; Apaldetti et al. 2011; Ezcurra and Apaldetti 2012).

Furthermore, recognising that a newly restricted Sauropoda required a new external specifier, Yates suggested *Melanorosaurus* (Yates 2007a,b). This new stem-based definition of Sauropoda as the most inclusive clade containing *Saltasaurus* but not *Melanorosaurus* has seen practical application in several recent topologies (Yates 2010; Ezcurra 2010; Taylor et al. 2010; Pol et al. 2011), and is certainly less problematic than Upchurch et al.'s (2007) retention of Sauropoda *sensu* Wilson and Sereno (1998) in which species of dubious sauropod affinity such as *Jingshanosaurus* and *Melanorosaurs* are regarded as sauropods purely by virtue of their exclusion from a monophyletic grouping of 'core prosauropods'. In concert with a more inclusive Sauropoda, Allain and Aquesbi (2008) suggested 'Gravisauria' to capture those forms traditionally regarded as Sauropoda *sensu stricto* (i.e., *Vulcanodon* and all taxa more advanced, but see below), although this name has thus far received only minimal application (see Yates et al. 2012).

Alternatively, Sereno (2007) has suggested the phylogenetic label 'Sauropodiformes' as a means of uniting basal sauropodomorphs currently occupying the middle-ground between 'true' sauropods and more basal massopodan taxa. Although in Sereno's (2007) original definition both *Jingshanosaurs* and *Mussaurus* (as taxa more advanced than his arbitrarily selected group of 'core prosauropods') were selected as joint anchor taxa of the least inclusive clade also containing *Saltasaurus*, Langer et al. (2010a) have subsequently simplified the situation by allocating *Mussaurus* as the exclusive basal anchor taxon for Sauropodiformes while simultaneously restricting the content of Sauropoda to the original node based definition of Salgado et al. (1997): "the most recent common ancestor of *Vulcanodon* and Eusauropoda and all of it descendents" (**fig. 2**). This expansion of Sauropodiformes, along with the concurrent restriction of Sauropoda, further reserves the latter term to those crown-ward taxa that share a graviportal, long-necked bauplan. As the full range of motion and precise locomotor strategy of these 'Sauropodiformes' is yet to have been unequivocally established, it may prove desirable to preserve a nomenclatural distinction between basal and derived sauropodomorphs that reflects the adoption of the characteristic 'sauropod' morphology.

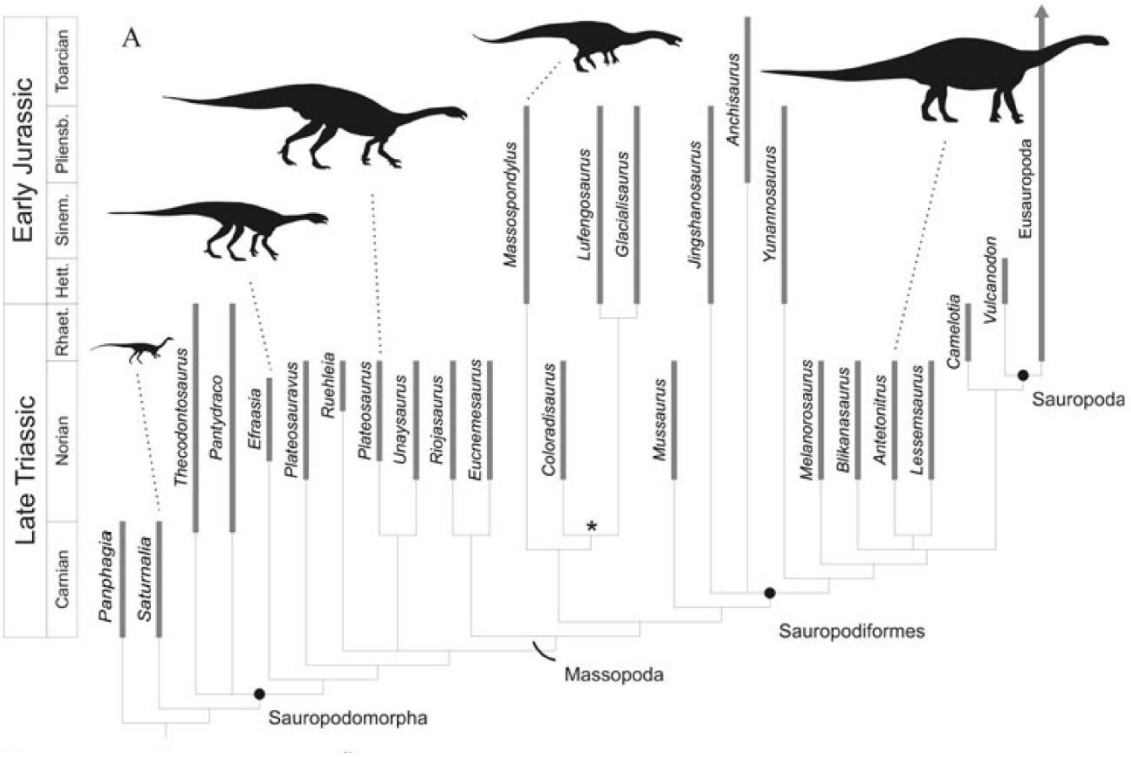

Fig.2. Preferred phylogeny of sauropodomorph relationships from Langer et al. (2010a: Fig. 16)

In conclusion, although the last few years have seen increased taxon sampling, improved resolution, more thorough hypothesis testing and perhaps more congruence between studies (with the monophyletic status of groups such as the Plateosauridae and Massospondylidae being established and expanded upon [Leal et al. 2004; Martinez 2009; Apaldetti et al. 2011]), the interrelationships between non-sauropodan sauropodomorphs remain in a state of flux. It is looking increasingly likely, however, that the common ancestor of Sauropoda shared a common ancestor with an array of late Triassic large-bodied sauropodiformes that in turn shared a common ancestor with a diverse group of basal sauropodomorph taxa.

1.4 THE FOSSIL EVIDENCE: CHARACTER-STATE DICHOTOMIES AND THE SAUROPODOMORPH/SAUROPOD TRANSITION.

The ancestor-descendant relationship between 'prosauropods' and sauropods had been hypothesised as early as 1920 by Huene, when he erected 'Prosauropoda' as an earlier, time-successive segment of a single anagenetic evolutionary lineage leading to Sauropoda. However, as the overlapping temporal distribution of 'prosauropods' and sauropods became increasingly evident throughout the century, the idea that they might represent separate, mutually exclusive lineages began to take hold. Thus, on the odd occasion that 'melanorosaurids' were put forward as potential sauropod ancestors (e.g. Romer 1956; Bonaparte 1986), any similarities between the two groups were ultimately dismissed as "superficial" (Upchurch 1997). Accordingly, a number of 'prosauropod' synapomorphies were subsequently erected in support of this stance, mainly centred on adaptations of the hand and foot that were believed to be irreversible and/or absent within basal sauropods (see Table 1.). However, the recent spate of relatively complete *Melanorosaurus* descriptions has only proven to underline and emphasise the close morphological relationship between this taxon and Sauropoda (Galton et al. 2005; Yates 2007b; Bonnan and Yates 2007).

This is emblematic of a greater trend within sauropodomorph studies of the last several years. The new phylogenetic paradigm (see above) has led to a more sophisticated understanding of the character distributions between Sauropodomorpha and Sauropoda. In short, a number of mutually exclusive synapomorphies attributed to both 'Prosauropoda' and Sauropoda are now understood to be considerably more inclusive than originally believed. The following provides a brief review of the anatomical data that has been most instrumental in breaking down the dichotomous reading of 'prosauropod' and sauropod relationships. Nevertheless, vast gaps remain in our knowledge of the transition from basal Sauropodomorpha to Sauropoda, mainly because taxon sampling is not as dense as in other parts of the tree and because many of the key taxa are incomplete specimens. These limitations will be acknowledged accordingly.

TABLE 1. Selected traditional synapomorphies listed for a mutually monophyletic Sauropoda and 'Prosauropoda'.

Sauropoda
1. At least four sacral vetebrae (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 1998).
2. Hyposphenal ridge on anterior caudal vertebrae (Upchurch 1995, 1998).
3. Columnar, obligatory quadrupedal posture with forelimb approximately 0.65% or more of hindlimb (Marsh 1878, Wilson and Sereno 1998; Upchurch 1998; Wilson 2002).
4. Humerus-to-femur ratio 0.7 or more (Romer 1956; Gauthier 1986; Wilson 2002).
5. Deltopectoral crest of the humerus reduced to a low crest (Wilson and Sereno 1998; Wilson 2002).
6. Proximal articular surface of the ulna triradiate with deep radial fossa and a reduced (or absent) olecranon process (Wilson and Sereno 1998; Wilson 2002).
7. Posterior margin of distal radius flattened for articulation with ulna (Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004).
8. Ischial peduncle of ilium low-to-absent (McIntosh 1990; Wilson and Sereno 1998; Wilson 2002).
9. Distal shaft of ischium blade-like (Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004).
10. Femural shaft elliptical in cross-section (Upchurch 1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al.
11. Both femoral fourth and lesser trochanters reduced to low ridges (Marsh 1878; Gauthier 1986; McIntosh 1990; Upchurch 1998; Wilson and Sereno 1998; Wilson 2002).
12. Ratio of tibia to femur length less than approx. 0.7 times the length of the femur (Upchurch 1998, et al. 2004).
13. Astragalus lacking fossa and foramina at base of ascending process (Wilson and Sereno 1998; Wilson 2002).
14. Distal tarsals three and four absent or fail to ossify (Gauthier 1986; Upchurch 1998; Wilson and Sereno 1998; Wilson 2002).
15. Metatarsal III-to-tibia ratio less that 0.4 (Upchurch et al. 2004).
16. Proximal surfaces of metatarsal I and V subequal to, or larger than, metatarsal II, III and IV (Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004).
17. Ratio of length of metatarsal V to metatarsal IV at least 0.7 (Van Heerden 1978; Gauthier 1986; Wilson and Sereno 1998; Wilson 2002).
18. Pedal digit I ungual longer the metatarsal I and deep and narrow (sickle shaped) (Wilson and Sereno 1998; Wilson 2002).
Prosauropoda
1. Secondary antorbital fossa wall/lateral lamina along ventral margin of antorbital fossa (Sereno 1999, 2007; Upchurch et al. 2007b).
2. 5-6 large neurovascular foramina on the lateral surface of the maxilla (Sereno 1999, 2007; Upchurch et al.
3. Strap-like ventral process of the squasmosal (Sereno 1999, 2007; Galton and Uchurch 2004).
4. Ridge on the lateral surface of the dentary (Galton and Upchurch et al. 2004; Upchurch et al. 2007b).
5. Inset first dentary tooth (Sereno 1999, 2007; Galton and Upchurch et al. 2004; Upchurch et al. 2007b).
6. Axial postzygapophyses flush with the posterior end of the centrum (Sereno 1999, 2007; Upchurch et al. 2007b).
7. Absence of prezygodiapophyseal laminae on posterior dorsal neural arches (Galton and Upchurch et al. 2004).
8. Deltopectoral crest of the humerus perpendicular to the transverse axis of the distal condyles (Sereno 1999, 2007; Galton and Upchurch et al. 2004; Upchurch et al. 2007).
9. Deltopectoral crest equal-to or more that 50% the total length of the humerus (Sereno 1999, 2007).
10. Transverse width of the distal condyles of the humerus greater than 0.33 times the total length of the bone (Upchurch et al. 2007b).
11. Lateral end of first distal carpal overlaps second distal carpal so that the proximolateral base of the first metacarpal is inset into the carpus (Sereno 1999, 2007; Upchurch et al. 2007).
12. Proximal width of metacarpal I no less than 0.65 times metacarpal length (given as 1.0 in Upchurch et al. 2007b) (Sereno 1999, 2007).
13. Proximoventral 'heel' on first phalanx of manual digit I (Sereno 1999, 2007; Galton and Upchurch et al. 2004; Upchurch et al. 2007b).
14. Proximal and distal surfaces of first phalanx of manual digit I twisted by at least 45 degrees with respect to one-another (Sereno 1999, 2007; Galton and Upchurch et al. 2004; Upchurch et al. 2007).
15. Ischial distal shaft sub-triangular in cross-section (Sereno 1999, 2007).
16. Lateral surface of metatarsal II is concave rendering proximal surface hourglass-shaped (Sereno 1999, 2007; Upchurch et al 2007b).
17. Transverse width of the proximal end of metatarsal IV at least 3.0 times its dorsovental depth (scaled down to 2.0 in Upchurch et al. 2007b) (Sereno 1999, 2007).
18. Metatarsal V significantly reduced in size relative to the rest of the metatarsus (Charig et al. 1965; Cruickshank

The region that is least well known, and hence least informative regarding the step-wise acquisition of sauropod traits, is that of the skull. Although the skulls of relatively basal taxa such as *Lufengosaurus* (Barrett et al. 2005), *Yunnanosaurus* (Barrett et al. 2007) and *Massospondylus* (Gow et al. 1990) are known from the lower Jurassic deposits of both China and South Africa, the only basal 'true' sauropod with a substantial degree of cranial material preserved is *Shunosaurus lii* from the ?Bajocian of China (Zhang 1988; Chatterjee and Zheng 2002). Although a complete skull has recently been referred (and fully described) to the relatively advanced Late Triassic massopodan taxon *Melanorosaurus*, the osteology of this specimen is largely plesiomorphic, lacking the anteroposterior shortening of the skull so typical of Sauropoda (Yates 2007b) (although Rauhut et al. [2011] suggest that the skull in question is strongly compacted dorsoventrally and that the reconstruction of Yates [2007b] considerably underestimates its height). Therefore, the stratigraphic interval separating *Melanorosaurus* from *Shunosaurus* covers approximately 25+ million years in which little well-preserved cranial material is known. Nonetheless, several partial specimens recently described from Jurassic deposits in South Africa (Yates et al. 2010), China (Upchurch et al. 2007a), and Morocco (Allain and Aquesbi 2008) hint at the continuity of a number of cranial characteristics between non-sauropodan sauropodomorphs and Sauropoda.

Chinshakiangosaurus, a poorly known specimen of putative basal sauropod affinity from the Fengjiahe Formation (Lower Jurassic) of China preserves an entire left dentary. Although the taxonomy of this specimen remains equivocal in the absence of a complete description of both its cranial and post-cranial remains, *Chinshikiangosaurus* is interesting because while it shares a number of apomorphies with Sauropoda, it retains a lateral ridge on the dentary (Upchurch et al. 2007a). This ridge is hypothesised as being the anchor for a fleshy cheek and has long been regarded as a classic synapomorphy of 'Prosauropoda', whereas this gape-restricting attachment was thought to be plesiomorphically absent in Sauropoda (Galton and Upchurch 2004; Upchurch et al. 2007b). Of greater potential significance is the absence of this feature in the derived massopodan taxon *Aardonyx celestae,* a recently described addition to the sauropodomorph assemblage of the Upper Elliot Formation of South Africa (Yates et al. 2010). The presence of a lateral dental ridge in a probable basal sauropod and its absence in a non-sauropodan sauropodomorph suggests an unexpectedly wide variety of specialised feeding strategies within Sauropodomorpha as well as the

complex mosaic-like pattern of character acquisition at the sauropodomorph/sauropod boundary.

Other features listed as exclusive characters of the 'prosauropod' skull, such as an inset first dentary tooth (hypothesised as a correlate of a keratinous lower beak [Sereno 2007]), a unique array of neurovascular foramina on the lateral surface of the maxilla, and a secondary antorbital lamina (= the external ventral rim of the anteorbital fenestra is raised above the level of the internal ventral rim) remain purely speculative until more good quality early sauropod material is unearthed (Sereno 1999, 2007; Upchurch et al. 2007a). However, it is possible that the loss of the small platform anterior to the first dentary tooth in Sauropoda may simply relate to the transverse widening of the jaw typical of that group (Yates 2007b; Rauhut et al. 2011).

The now more fully described *Tazoudasaurus naimi* from the early Middle Jurassic of Morocco is also significant in preserving fragmentary cranial material that suggests that basal sauropods shared a number of features with taxa nested deep within basal Sauropodomorpha (Allain and Aquesbi 2008). These pertain to features of the parietal (absence of the anterolateral process contacting the postorbital, thus allowing the frontal bone to contribute to the supratemporal fenestra), the quadrate (upper two thirds bent laterally as in *Plateosaurus* and lacking the quadrate fossa seen is other sauropods), and dentary (depth of mandibular symphysis intermediate between the thin sauropodomorph condition and the dorsoventrally expanded morphology of sauropods, presence of 18 teeth). Additionally, the putative presence of several sauropod-like features in the small massopod *Anchisaurus polyzelus* (e.g. frontal exclusion from the supratemporal fenestra, infratemporal fenestra drawn forward under the orbit, wrinkled tooth enamel) further hints at the mosaic patterning and potential homoplasy that appears to have punctuated either side of the basal sauropodomorph/sauropod divide.

Thus, although a truly intermediate exemplar still awaits discovery, it seems likely that increased sampling of the poorly known early Jurassic period of Sauropod cranial evolution will only strengthen the morphological link between 'prosauropods' and sauropods. Unsurprisingly, the post-cranial skeleton, in preserving a more complete sequence between

non-sauropodan sauropodomorphs and Sauropoda, collected the largest number of mutually exclusive 'prosauropod vs. sauropod' synapomorphies.

Axial skeleton: Although never having been formalised into a series of mutually exclusive character-states, features related to the pneumaticity of the pre-sacral vertebral column have significant phylogenetic implications regarding the hypothesised ancestor-descendant relationship of 'Prosauropoda' and Sauropoda. An avian-like system of air-sacs and bone-invading diverticula has long been recognised as a possible explanation for the characteristic cavity-pocked appearance of sauropod vertebrae (Seeley 1870, Janesch 1947). As well as representing a possible evolutionary solution to the problem of tracheal dead-space imposed by an improbably long neck (by facilitating a unidirectional air-flow as opposed to the bellows-like lungs of extant reptiles and mammals), a pulmonary air-sac system would have also had significant implications for both skeletal mass-reduction and thermoregulation (Wedel et al. 2000, 2003a,b, 2006, 2009; O'Connor 2006).

It was originally believed that the vertebrae of all 'prosauropods' were apneumatic – that is, the diverticula, if present at all, did not penetrate into the bone itself, failing to produce the characteristic sharp-rimmed fossae and subfossa displayed by a number of advanced sauropod genera (e.g. *Apatosaurus*; *Brachiosaurus*) (Wilson 1999; Wedel 2003a,b, 2005, 2009; O'Conner 2006; Yates et al. 2012). However, a recent study by Yates et al. (2012) has shown the basal-sauropodomorph record to be punctuated with hitherto unrecognised examples of incipient pneumatic invasiveness. *Pantydraco caducus* (previously *Thecodontosaurus caducus*) represents the earliest known example of invasive diverticula in basal Sauropodomorpha with the appearance of weakly developed pneumatic-like features in the midcervical vertebra (Yates 2003a; *contra* Galton and Kermack 2010). Similarly, isolated specimens of *Plateosaurus* display pneumatic fossae on both the dorsolateral surface (AMNH 6810) and posterior infradiapophyseal fossa of posterior cervical vertebrae (SMNS F65), possibly representing "... independent, small–scale acquisitions of the ability for pneumatic diverticula to invade bone" (Yates at al. 2012:98).

These are the only known instances of pneumatisation of the cervical series in non-sauropodan sauropodomorph dinosaurs, with most other examples more commonly coming from the infradiapophyseal fossae (the fossae bound by the laminae that radiate out from

beneath the transverse processes in saurischian dinosaurs; see Wilson 1999) of the dorsal vertebral series. *Eucnemesaurus* displays a subtriangular subfossa at the deepest point of the posterior infradiapophyseal fossa of BP/1/6107, a posterior dorsal vertebra. *Aardonyx* also displays a posterior dorsal vertebra with a subfossa at the deepest point of its posterior infradiapophyseal fossa, this time a sharp-rimmed oval pit reaching 11mm in depth. And *Antetonitrus ingenipes* (the subject of the following osteological analysis) possesses large posterior infradiapophyseal subfossae on the neural arch of a mid-posterior dorsal vertebra, one of which is internally subdivided by an additional thin lamina. This evidence of pneumaticity in non-eusauropodan sauropodomorphs alludes to the development of an avian-style pulmonary air-sac system early in the evolution of Sauropodomorpha, possibly representing a synapomorphy of saurischian dinosaurs.

Wilson and Sereno (1998; see also Upchurch 1995, 1998) listed four or more sacral vertebrae as a synapomorphy of a mutually exclusive Sauropoda. Although they conceded that four sacral vertebrae had previously been observed in a specimen of *Melanorosaurus* (Van Heerden and Galton 1997), this was interpreted as the independent acquisition of a fourth sacral element, and not indicative of a close relationship between sauropods and 'melanorosaurids'. The plesiomorphic possession of three sacral vertebrae thus became diagnostic of 'prosauropods' (although there remains some confusion as to the precise patterning of the third sacral element which, although normally acquired from the dorsal series, has also been interpreted as a caudo-sacral in some specimens of *Plateosaurus* [Galton 2000; Galton and Upchurch 2000; Yates 2003; Moser 2003]). The discovery and further analysis of a relatively complete, fully articulate specimen of *Melanorosaurus* (NM QR3314: Yates 2007b) suggests that some specimens of that taxon may have possessed as many as five sacral vertebrae (an additional dorso-sacral plus a caudo-sacral).

However, the taxon that perhaps best illustrates the unexpectedly high distribution of this sacral character within sauropodomorpha is the recently described *Leonerasaurus taquetrensis* from the Early Jurassic Las Leoneras Formation of Central Patagonia (Pol et al. 2011). This particularly small and gracile specimen possesses both dorso-sacral and caudo-sacral elements, suggesting that the incorporation of additional vertebrae into the sauropod pelvis predated any marked increase in body size. The significance of *Leonerasaurus* in regards to the step-wise acquisition of the sauropodan bauplan remains contingent on its

precise phylogenetic relationships, and it is possible that this derived sacral feature may simply represent an isolated case of homoplastic convergence. However, as Pol et al. (2011) recovered *Leonerasurus* in a relatively derived position basal to *Melanorosaurus*, it is possible that, along with *Anchisaurus*, *Leonerasaurus* offers a glimpse of the unexpected diversity of body sizes that prefaced the early evolutionary history of Sauropoda.

Forelimb: A variety of synapomorphies of the forelimb have been proposed for both Sauropoda and 'Prosauropoda'. These generally pertain to structural characteristics of the humerus and manus, although the distinctive morphology of the sauropod ulna has been noted on numerous occasions (Wilson and Sereno 1998).

The ratio of humerus to femur length is of obvious interest when framing hypotheses regarding the functional significance of differential humeral lengths between 'bipedal' 'prosauropods' and 'quadrupedal' sauropods. Hence, various synapomorphic ratios of humerus to femur length have been proposed. Wilson (2002) suggested that a humerus that is elongated to at least 0.7 of the femur is diagnostic of Sauropoda. However, a number of traditional 'prosauropod' taxa display humerus/femur ratios that exceed 0.7 (e.g. *Riojasaurus*; *Anchisaurus*; *Melanorosaurus*), while eusauropodan taxa such as *Shunosaurus* clearly fall below this ratio. Alternatively, Yates et al. (2010) have suggested a ratio of 0.8, but this in turn excludes even more 'true' sauropod taxa, such as *Apatosaurus* (Rauhut et al. 2011). It is possible that the relative lengths of the entire fore- and hindlimb represent a more accurate measure of the changes in sauropodomorph limb dynamics (as this would take account of the concurrent lengthening of the elements of the antebrachium and manus in the forelimb and the relative shortening of the distal elements of the hindlimb). Accordingly, a forelimb/hindlimb ratio of at least 0.65 has also been suggested by Wilson and Sereno (1998) and Upchurch (1998) as synapomorphic of Sauropoda. The main problem with this metric, however, is not only the exceedingly rare preservation of entire appendicular elements in individual body fossils, but the questionable homology in situations where a similar ratio is achieved via the differential lengthening and/or shortening of different elements (e.g. the lengthening of the humerus vs. the lengthening of the antebrachium).

In terms of discrete 'prosauropod' synapomorphies of the humerus, a deltopectoral crest that is deflected at roughly 90 degrees relative to the transverse axis of the distal condyles whilst constituting at least half the total length of the bone has been cited on more than one occasion (Galton 1990; Sereno 1999; Galton and Upchurch; Upchurch et al. 2007b). However, the form and orientation of the deltopectoral crest has proven difficult to consistently score and can be widely variable even within a single genus (Remes 2008). Both Yates (2003a) and Remes (2008) have pointed out that the orientation of this delicate, protruding structure would have been particularly sensitive to geological pressures during preservation. As sauropods have a reduced deltopectoral crest, the chance that its defining angle might be exaggerated by sediment pressure is proportionately lessened (Yates 2003a). Yates (2003a) also pointed out that basal taxa such as *Thecodontosaurus* and *Anchisaurus* have relatively short deltopectoral crests. Additionally, the thin, sinuous deltopectoral crest of *Plateosauravus* extends for less than half the length of the humerus (Yates 2003b), as does the atypically short deltopoectoral crest of the recently described massospondylid *Adeopapposaurus* (Martinez 2009), further indicating the chequered distribution of this character within Sauropodomorpha. *Plateosauravus* is also interesting given the transverse width of its distal condyles is less than a third of the total length of the humerus – the opposite of the 'prosauropod' condition (Upchurch et al. 2007b).

Wilson and Sereno (1998) cited the tri-radiate form of the proximal ulna as diagnostic of Sauropoda. Although the sauropod ulna is distinctive compared to its more basal sauropodomorph outgroups - especially regarding the deep radial fossa bound by either side by finely bowed extensions of bone – the intermediate morphology of basal taxa such as *Melanorosaurus* (Bonnan and Yates 2007), *Lessemsaurus* (Pol and Powell 2007) and *Antetonitrus* (Yates and Kitching 2003) is now well known. However, the absence of an olacrenon process in all known basal sauropods appears to represent a legitimate derived character of that group.

The manus presents perhaps the most obvious point of dissimilarity between Sauropoda and all non-sauropodan sauropodomorphs. Unsurprisingly, the unique architecture of the 'prosauropod' hand resulted in the establishment of several relatively robust synapomorphies (e.g., Sereno 1999; 2007). However, in a similar situation to that of the sauropodomorph skull, a considerable temporal gap (approx. 20 - 30 million years) exists

between the well-known morphology of the 'prosauropod' hand and the first occurrence of preserved manus material in the early Middle Jurassic sauropods *Tazoudasaurus* and *Shunosaurus*.

As noted by Sereno (1999; 2007) the 'prosauropod' manus is organised with the first metacarpal inset into the carpus. In this configuration distal carpal II articulates with metacarpal I proximolaterally, completely precluding the second metacarpal from making any contact with the enlarged distal carpal I – an arrangement generally absent in all known sauropods. Yates (2003a) has correctly pointed out that available figures for the manus of *Thecodontosaurus antiquus* (Benton et al. 2000), *Anchisaurus* (Galton 1976) and *Riojasaurus* (Bonaparte 1972) depict a manus in which the proximal surface of metacarpal I is flush with the rest of the metacarpus. However, the vast majority of known basal sauropodomorph taxa have the first metacarpal inset into the carpus, and its absence in the three aforementioned taxa implies either a series of independent reversals or erroneous reconstruction and/or preservation within the available literature (see also Sereno 2007). However, an articulated manus of a juvenile specimen of the basal sauropod *Tazoudasaurus* (Allain and Aquesbi 2008: Text-Fig 23) shows the proximal portion of the first metacarpal clearly raised above the proximal row of the remaining metacarpus. Although the second distal carpal is either unpreserved or lost by that point in sauropodomorph evolution, the configuration of the carpus as figured in the reference above suggests that the first metacarpal of *Tazoudasaurus* was inset into the carpus in a manner similar to that seen in 'prosauropods'.

In association with the inset first metacarpal 'prosauropods' also possess a first manual phalanx in which the distal condyles are twisted at roughly 45–60 degrees with respect to the proximodistal axis of the bone (Galton and Upchurch 2004). This rather marked ventrolateral twisting results in a first manual ungual that could be hyper-extended, potentially as a means of keeping the pollex raised from the substrate during sporadic periods of quadrupedal locomotion and/or an adaptation towards increased dexterity when feeding. The mobility of the 'prosuropod' pollex is also evident in the expansive articular ginglymus of the proximal first phalanx; the resultant concavity creates a proximoventral 'heel' that extends further proximally than the dorsal lip. None of these features are observable within the current record of sauropod dinosaurs from the Jurassic onwards

(although Yates [2003a] has suggested that a proximal 'heel' is primitively diagnostic of Saurischia as a whole). However, as stated above, the early evolution of the sauropod manus is poorly sampled. It is possible that many of the features of the 'prosauropod' hand – including a proximally widened articular surface of metacarpal I – are obscured by the substantial weight-bearing modifications that occurred as the grasping hand of more basal sauropodomorphs underwent the transition towards graviportal locomotion.

Pelvic girdle and hindlimb: The shape of the distal ischial shaft (in cross-section) has been used to characterise both Sauropoda (dorsoventrally flattened or 'bladelike': Wilson and Sereno 1998; Wilson 2002) and 'Prosauropoda' (subtriangular: Sereno 1999). However, this character appears to have had a complex distribution amongst both sauropodomorphs and their immediate outgroups. Flattened ischial blades were the primitive condition of Dinosauromorpha (Yates 2004), and although a number of basal sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*; *Lufengosaurus*) exhibit the subtriangular condition (seen also in Theropoda), *Anchisaurus*, *Leonerasaurus* and *Thecodontosaurus* appear to have retained the plesiomorphic state or secondarily reversed back to it (Yates 2003a; 2004; Pol et al. 2011). Furthermore, Sauropod taxa such as *Vulcanodon* and *Tazoudasaurus* clearly display subtriangular distal ischia. Given the confusing and inconsistent patterning of this character, it is probable that flattened, ovate ischial shafts represent an exclusive synapomorphy of neosauropods alone within Sauropoda (Yates 2003a).

The differences in the femoral architecture of 'prosauropods' and sauropods are well known, with the elliptical (as opposed to sub-circular) cross-section of the femoral shaft becoming established early on as a major diagnostic character of Sauropoda (McIntosh 1990; Wilson and Sereno 1998; Wilson 2002). That a similar – albeit less developed – transverse widening is observed in the femur of *Melanorosaurus* was dismissed as either a 'superficial' similarity or a convergent acquisition (Upchurch 1997). However, the discovery and in-depth descriptions of additional transitional taxa such as *Aardonyx* (Yates et al. 2010), *Antetonitrus* (Yates and Kitcjing 2003), *Camelotia* (Galton 1998) and *Lessemsaurus* (Pol and Powell 2007) which display varying degrees of this ellipsoid architecture in conjunction with a sauropod-like straightening of the femoral shaft only emphasised the step-wise nature of this character within Sauropodomorpha. The majority of these

transitional taxa also share the sauropod-like migration of the major trochanters (i.e. lesser; fourth) to derived positions on the femoral shaft.

As is the case with manus and the forelimb, traditional synapomorphies of the 'prosauropod' hindlimb are dominated by features of the pes. Classically, the reduction of the paddle-shaped fifth metatarsal was considered an irreversible feature of the 'prosauropod' foot (Charig et al. 1965; Cruickshank 1975; Van Heerden 1978, 1997; Galton 1990). However, Yates (2003a) has pointed out that the re-enlargement of a structure that is still present, or still genetically coded for, is quite possible. This phenomenon is well-known within the Dinosauria, with the reversal in the reduction of pedal digit I in therizinosauroid coelurosaurs representing perhaps the best known example (Kirkland et al. 2005). Additionally, examination of the available figures for the basal sauropod taxa *Vulcanodon* and *Shunosaurus* suggests that these forms possessed a fifth metatarsal that was transitional between non-sauropodan sauropodomorphs and Sauropoda (Cooper 1984; Zhang 1988; see also Sereno 2007).

Sereno (1999; recently reiterated by Upchurch et al. 2007b), drew attention to the biconcave form of proximal metatarsal II as a potential synapomorphy of 'prosauropoda.' In 'prosauropods' the medial and lateral margins of the proximal articular surface of the second metatarsal are concave for the reception of the first and third metatarsals, respectively. This arrangement is unique among dinosaurs, with the primitive condition tending towards a rectangular proximal metatarsal II with flat contact surfaces (Sereno and Arcucci 1994; Yates 2003a). Sauropods, while possessing a contact area for the reception of the first metatarsal that is equally concave to the same surface in 'prosauropods', apparently lacked the concurrent concavity on the lateral surface. However, the lateral concavity is generally proportionally much shallower than the medial, and specimens of *Plateosaurus* with negligible lateral concavities demonstrate that this embayment is mostly the product of a slight emargination of the proximolateral corners of the bone – a feature that would not require much alteration to present the undefined condition seen in the basal sauropod *Vulcanadon* (Cooper 1984). A biconcave proximal metatarsal II in the sister taxon of *Vulcanodon*, *Tazoudasurus*, further complicates the distribution of this character and Yates (2003a) has suggested that the concave medial surface alone represents an ambiguous synapomorphy of Sauropodomorpha.

Sereno (1999) also suggested a fourth metatarsal with the transverse width of its proximal surface being three times as broad as its dorsoventral depth as synapomorphy of 'Prosauropoda'. However, Yates (2003a) has correctly pointed out that this measurement is exclusive to *Massospondylus* alone within Sauropodomorpha. Therefore, perhaps unsurprisingly, this was scaled down to a proximal surface that was more than twice as wide as its dorsoventral depth by Upchurch et al. (2007b). As this new ratio also applies to the basal sauropods *Vulcanodon* and *Tazoudasurus* it cannot be said to be supportive of 'prosauropod' monophyly (Cooper 1984; Allain and Aquesbi 2008).

From the above review of basal sauropodomorph systematics, it is clear that a comprehensive understanding of the character-state relationships between basal Sauropodomorpha ('prosauropods') and Sauropoda continues to be obscured by poor preservation, complex character-state distributions and a series of potential reversals. In regards to this last point, Upchurch et al. (2007b) have drawn attention to a number (approximately twenty) of derived character states that originate within basal sauropodomorphs and then reverse at nodes in basal Sauropoda. However, as discussed above, several of these (e.g. features of the humerus and metatarsus) are shown to be more inclusive than previously thought, and a great number of other 'reversals' may simply pertain to the changes that the sauropodomorph bauplan underwent in the transition from a predominantly bipedal form of locomotion to a quadrupedal one. The significance of *Antetonitrus ingenipes* to the adaptive and phylogenetic issues reviewed above forms the principal investigative focus of the following study.

2. METHODS and MATERIALS

***Terminology*:** The current work employs traditional anatomical and directional terms over veterinarian alternatives (Wilson 2006). ‘‘Anterior’’ and ‘‘posterior’’, for example, are used as directional terms rather than the veterinarian alternatives ‘‘rostral’’ or ‘‘cranial’’ and ‘‘caudal’’. When describing directional orientations, the bone is assumed to have been held along its closest horizontal or vertical axis (e.g. the scapula is presented as being completely vertically oriented). Although it is likely that a number of elements – especially those of the pectoral girdle and forelimb – were held at angles of varying obliqueness to the substrate, for the sake of terminological simplicity no attempt to recreate the precise living-position of either the appendicular or axial skeleton was undertaken (*contra* Remes 2008).

Throughout the description and subsequent discussion a number of clade names are mentioned. These are outlined in Table 2. The definition of Sauropoda is still somewhat in flux, with both Sauropoda *sensu* Yates (2007a,b) and Sauropoda *sensu* Salgado et al. (1997; see also Langer et al. 2010a) experiencing regular application in recent studies. However, for reasons that will be outlined in the text, the latter is favoured here.

TABLE 2. Clade names and their sources mentioned throughout the text

CLADE	DEFINITION	SOURCE
Sauropodomorpha	The most inclusive clade including *Saltasaurus* but not *Tyrannosaurus rex*	Taylor et al. 2010
Massopoda	The most inclusive clade that contains *Saltasaurus* but not *Plateosaurus engelhardti*	Yates 2007a,b
Massospondylidae	The most inclusive clade containing *Massospondylus* but not *Plateosaurus engelhardti* or *Saltasaurus*	Sereno 2007
Sauropodiformes	The most inclusive clade containing *Saltasaurus* but not *Massospondylus*	Defined within
Sauropoda	The least inclusive clade containing *Vulcanodon* and Eusauropoda	Salgado et al. 1997, Langer et al. 2010a
Eusauropoda	The least inclusive clade containing *Shunosaurus* and *Saltasaurus*	Upchurch et al. 2004
Neosauropoda	The least inclusive clade containing *Diplodocus* and *Saltasaurus*	Wilson and Sereno 1998

***Comparative Taxonomy*:** The comparisons with basal Sauropodomorpha and Sauropoda made in the following description were based on both the literature and on personal observation of specific taxa detailed in Table 3.

TABLE 3. List of comparative taxa used in present analysis. Specific accession numbers represent specimens viewed firsthand by the author, whereas all other references were drawn from the literature listed within the table.

TAXON	SOURCE(S)
Sauropodomorpha	
Saturnalia tupiniquim	Langer 2003; Langer et al. 2007
Thecodontosaurus antiquus	Benton et al. 2000
Pantydraco caducus	Yates 2003a
Plateosauravus cullingworthi	van Heerden 1979
Plateosauria	
Unaysaurus tolentinoi	Leal et al. 2004
Plateosaurus engelhardti	von Huene 1926; Moser 2003; Yates 2003, Mallison 2010a,b
Massopoda	
Eucnemesaurus fortis	BP/1/6107; Yates 2007a
Riojasaurus incertus	PVL 3808; Bonaparte 1972
Lamplughsaura dhamaramensis	Kutty et al. 2007
Seitaad ruessi	Sertich and Loewen 2010
Leonerasaurus taquetrensis	Pol et al. 2011
Massospondylidae	
Massospondylus carinatus	BP/1/4377, 4693, 4924, 4934, 4998, 5000, 5241; Cooper 1980
Coloradisaurus brevis	PVL 5904 (field no. 6); Apaldetti et al. 2012
Lufengosaurus hueni	Young 1941
Adeopapposaurus mognai	Martinez 2009
Glacialisaurus hammeri	Smith and Pol 2007
Sauropodiformes	
Yunnanosaurus huangi	Young 1942
Jingshanosaurus xinwaensis	Zhang and Yang 1994
Aardonyx celestae	BP/1/386; various elements catalogued BP/1/5379 - 6893
Anchisaurus polyzelus	Galton 1976; Yates 2004a; Yates 2010
Melanorosaurus readi	NM QR1551, 3314; Galton et al. 2005; Bonnan and Yates 2007
Blikanasaurus cromptoni	Galton and van Heerden 1998; Yates 2008
Lessemsaurus sauropoides	PVL 4822; Pol and Powell 2007
Gongxianosaurus shibeiensis	He et al. 1998
Sauropoda	
Isanosaurus attavipachi	Buffetaut et al. 2000
Vulcanodon karibaensis	Cooper 1984
Tazoudasaurus naimi	Allain and Aquesbi 2008
Spinophorosaurus nigerensis	Remes et al. 2009
Eusauropoda	
Shunosaurus lii	Zhang 1988
Barapasaurus tagorei	Bandyopadhyay et al. 2010
Omeisaurus tianfuensis	He et al. 1988
Mamenchisaurus	Young and Zhao 1972
Cetiosaurus oxoniensis	Upchurch and Martin 2003

Institutional abbreviations: AMNH, American Natural History Museum, New York, USA; BPI, Bernard Price Institute, Johannesburg, South Africa; FMNH, Field Museum of Natural History, Chicago, Illinois; GPIT, Institute for Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany (*Formerly Geologisch-Paläontologisches Institut Tübingen);* IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; NM QR, National Museum, Bloemfontein, South Africa; PULR, Paleontologıa, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Instituto Miguel Lillo, Tucuman, Argentina; SAM-K, Iziko-South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum fur Naturkunde Stuttgart, Stuttgart, Germany; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZDM T, The Chongqing Natural History Museum, Chongqing, China.

Cladistic analysis

A cladistic analysis was conducted in order to investigate the phylogenetic implications of the new anatomical knowledge of the *Antetonitrus* material. This analysis was drawn from the data matrix initially employed by Yates (2007b), and subsequently modified (in terms of the revision and addition of both taxa and characters) by Smith and Pol (2007), Yates et al. (2010), Yates (2010), and Apaldetti et al. (2011). Ezcurra (2010) (modified later by Novas et al. 2011) also used a modified version of this matrix. The additional 17 characters suggested by Ezcurra (2010) were not employed in the current analysis, because, of the 17 additional characters proposed by him, only 16 are present in the actual matrix (i.e. there are 377 character instead of the stated 378). It was therefore difficult to trace what characters were included and which one was not. Nonetheless, a number of the modifications to *Guiabasaurus*, *Chindesaurus*, *Herrerasaurus*, *Eoraptor* and *Saturnalia* suggested by Ezcurra (2010) are incorporated here. *Ignavusaurus* was deliberately excluded as its status as valid taxon remains controversial with some authors suggesting it is synonymous with *Massospondylus* (Yates et al. 2011). *Sarahsaurus* was also excluded due to a conspicuously high number of autopomorphic character states (many converging on the sauropodan condition), some of which are of questionable validity (e.g., the lack of an olecranon process, a 'blunt' preacetabular process; Rowe et al. 2010).

Modifications in the current analysis focused primarily on the scoring of characters in *Antetonitrus*. However, first hand examination of the closely-related *Lessemsaurus* (PVL 4822) also allowed for reassessing a number of characters in that taxon (see Appendix).

Archosaurian (i.e. Crurotarsia/Dinosauromorpha/Ornithischia/Theropoda) outgroup relationships recovered by Yates (2007a,b, 2010), Ezcurra (2010) and Apaldetti et al. (2011) exceeded the scope of the current analysis and hence the character codings for these groups were not personally examined. Broader sauropodomorph ingroup relationships were also not systematically reassessed due to time constraints, and any changes were made on an *ad hoc* basis. The character-taxon matrix represented by 54 taxa and 361 characters was analysed using TNT 1.1 (Goloboff et al. 2008) using a heuristic search of 1000 replicates of Wagner trees followed by TBR branch swapping with 10 trees saved per replication. All 36 multistate characters coded as ordered in Yates (2007a,b) and Yates et al. (2010) were kept as such. Characters were equally weighted.

3. RESULTS

3.1 SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Sauropodomorpha Huene, 1932

Massopoda Yates 2007

Sauropodiformes Sereno 2007

Antetonitrus ingenipes Yates and Kitching 2003

Etymology: "The generic name is from Latin, ante (before); tonitrus (thunder) and refers to the early occurrence of this sauropod relative to '*Brontosaurus'* (Greek, thunder lizard) one of the most familiar sauropod names. The species name is from Latin, ingens (massive) and pes (paw, or foot) and refers to its robust hands and feet" (Yates and Kitching 2003: 1754).

Locality and Horizon: The specimen was discovered in 1982 by James Kitching in the saddle between the farms Welbedacht 611 and Edelweiss 698, Ladybrand District, Free State, South Africa (now within the boundary of Broken Slopes) (29˚06'24" S; 27˚19'10"E). A recent visit to the type locality by the author revealed that this saddle exposes a substantial portion of the upper strata of the Lower Elliot Formation. Although the precise excavation site could not be located, there is little reason to doubt Kitching and Raath's (1984) pronouncement that the remains came from "low down in the Elliot Formation" – and hence from within the bounds of the Lower Elliot Formation. In the past, the Lower Elliot Formation has been assigned to the Carnian stage (Gauffre 1993; Galton and van Heerden 1998; Anderson et al. 1998) but the current consensus places it within the Norian, with the possibility that its upper sediments may even be Rhaetian in age (Lucas and Hancox 2001; Bordy et al. 2004, 2005; Irmis 2010).

Holotype: Although the holotype as defined by Yates and Kitching (2003) is represented by disarticulated material, we can conservatively show that some of the holotype material pertains to at least one seperate individual. Subject to article 73.1.5. of the International Code of Zoological Nomenclature, we revise the holoype and referred material as listed below.

The updated holotype **BP/1/4952** includes: a cervical centrum, three dorsal neural arches, four dorsal centra; a ?caudosacral neural arch, ?ten caudal vertebrae, two dorsal ribs, chevrons, left scapula, right humerus, both ulnae, right radius, right metacarpal I, left metacarpal II, right manual phalanx I1, left pubis, left femur, left tibia, left fibula, left metatarsal I, right metatarsal II, left metatarsal III, right metatarsal V, two pedal phalanges, right pedal ungual I, right pedal ungual ?III. The monospecific status of BP/1/4952 is supported by the closely associated, in situ nature of the bones upon discovery (Kitching and Raath 1984; see Fig. 1).

Duplicates of the left scapula and left metacarpal II, assigned to the holotype by Yates and Kitching (2003), are from an animal of similarly large dimensions to the rest of the holotype material. We remove these from the holotype and assign them the new catalog number **BP/1/4952c**.

BP/1/4952b: The remaining material from the primary Antetonitrus quarry is comprised of duplicate elements that, while measurably smaller than the holotype, display an identical morphology (with the exception of the fibulae, but see Description). This duplicate material essentially comprises the 'paratype' individual of Yates and Kitching (2003), and on this basis we retain the catalogue number asigned in that paper (BP/1/4952b). Included is a posterior dorsal neural arch, ?two caudal vertebrae, a right scapulae, right humerus, right ulna, right radius, and right fibula.

***Diagnosis*:** A robust, large-bodied transitional sauropodomorph (= Sauropodiformes). In addition to the features given in Yates and Kitching (2003), *Antetonitrus ingenipes* can be further distinguished from most non-sauropodan sauropodomorphs by the following unique combination of characters (* = autopomorphy): high dorsal neural spines that are over half the total height of the neural arch *; dorsal neural arches that are over twice as tall as all associated dorsal centra*; pneumatic subfossae in the posterior infradiapophyseal fossae of the mid-posterior dorsal neural arch; ?presence of caudosacral vertebrae; single articular facet on proximal chevrons*; broadly expanded dorsal scapular blade; head of humerus vaulted and expanded posteriorly; medial tuberosity of the humeral head reduced and slightly inturned*; delicate, non-sinuous deltopectoral crest; medial deflection of the anterior process of the proximal ulna*; incipient radial fossa on the proximal ulna; distinct bifurcated tubercle on the lateroventral edge of the shaft of metacarpal II; femoral shaft that is elliptical in cross-section and reduced in lateral sinuosity; a laterally displaced lesser trochanter of the femur that is visible in posterior view; a fourth trochanter that is located on the medial edge of the mid-shaft of the femur; anteroposterior length of the proximal surface of the tibia over twice its transverse width and roughly level with the horizontal plane; descending process of the distal tibia compressed laterally so that the anterior ascending process is visible in posterior aspect; robust, entaxonically spreading pes; metatarsal III less than 40% length of tibia; length of pedal ungual I greater than metatarsal I.

Additionally, *Antetonitrus* can be distinguished from more advanced sauropodan taxa with reference to the following features: amphiceolous vertebral centra; deltopoectoral crest

that is oriented perpendicularly to the transverse axis of the distal condyles and represents at least half of the total length of the humerus; deep inter-condylar depression (=cuboid fossa) on the distal humerus; large olecranon process of the ulna; short, robust antebrachium; shortened metacarpus with an axially twisted phalanx I.1; iliac peduncle of the proximal pubis anteriorly sub-confluent with the transversely oriented pubic apron; a hypertrophied M. caudofemoralis brevis insertion*; cnemial crest of the tibia transversely broad and anteriorly projecting; metatarsal V reduced in size relative to other metatarsals.

Referred material:

NM QR1545: an assemblage of approximately three individuals representing two distinct size-classes recovered from the Excelsior District of the Free State. It consists of a large right humerus of similar relative proportions and absolute size to BP/1/4952; two small right ulnae (both missing the proximal and distal ends); left and right ilia (of slightly different size and markedly different preservation); two femora including a large left (heavily damaged) and large right that is once again of the same general relative and absolute proportions as BP/1/4952 (but missing the major portion of the femoral head); three tibia, a small (incomplete) right element, and two large, subequally sized left (complete) and right (incomplete) elements; three fibulae, a large right and two sub-equally sized, smaller elements of both sides.

Where observable (the condition of NM QR1545 is comparably poorer than that of BP/1/4952), the above bones display the same diagnostic criteria and basic morphology as that listed above for BP/1/4952. This provides a strong case for their referral to *Antetonitrus ingenipes*. However, differential preservation (i.e. in colour, quality of preservation) amongst many of the elements suggests that NM QR1545 may not represent an associated assemblage of bones, but that fossilised 'float' from the surrounding area was collected alongside other, *in situ*, material. However, given that a detailed account of the collection of NM QR1545 was never recorded, this is impossible to substantiate.

BP/1/5091: recovered from the *Antetonitrus* type locality two years after the collection of BP/1/4952, BP/1/5091 represents sacral material from a juvenile specimen (as indicated by

the unfused neuro-centro/sacrocostal juncture) and includes a sacral neural arch from either of the primordial sacral vertebrae, a partial ?caudosacral neural arch, and the centra from what was potentially the dorsosacral vertebra. The referral of these elements to *Antetonitrus* is based mainly on the transverse dorsal expansion of the neural spine of the primordial vertebrae as well as the wide, equilateral triangle-shaped hyposphene. Additionally, the partial caudosacral neural arch very closely resembles the same element in BP/1/4952.

The 'Bloem Dino': Although no formal referral of this vast sum of material to *A.ingenipes* is offered here, several analyses that have made their way into both the published and unpublished literature suggest that amongst this material is an animal very similar, if not identical, to *Antetonitrus ingenipes* (Ellenberger and Ellenberger 1956; Ellenberger and Ginsburg 1966; Gauffre 1993, 1996). Between 1955 and 1970 the brothers Ellenberger excavated a dinosaur quarry of unprecedented richness from the Lower Elliot Formation of Maphutseng, Lesotho. This material represents a large sauropodomorph that has, in turn, been referred to '*Euskelosaurus'* (Gauffre 1993) as well as providing the basis for the erection of a novel taxon ('*Kholumolumosaurus*') in an unpublished PhD thesis (Gauffre 1996). Now divided between the National Museum in Bloemfontein, the University of Cape Town, and the Museum National d'Histoire Naturelle in Paris, it is impossible to say at this point whether this assemblage represents a single species, or if there are multiple taxa present. Clearly, future studies are required to establish a comprehensive profile of the Maphutseng assemblage, and to determine how much of it – if any – is referable to *Antetonitrus*. Accordingly, some of this material is currently under study by a student from the University of Cape Town.

4. ANATOMICAL DESCRIPTIONS

4.1 AXIAL SKELETON

4.1.1 CERVICAL VERTEBRAE

The neck of *Antetonitrus* is represented by a single cervical centrum (**Fig.3**). A middle to posterior position in the cervical sequence is likely because the parapophyses are clearly visible just above mid-height and set slightly back from the anterior margin of the centrum. The centrum has experienced post-depositional compression so that the ventral surface has been obliquely displaced relative to the dorsal surface, deflecting the articular facets laterally. However, the basic morphology of the centrum remains preserved.

The centrum of is fairly typical of those seen in all non-eusauropodan sauropodomorphs, being both amphicoelous and acamerate. Given the post-depositional distortion of the bone, it is difficult to establish a precise measure of the relationships of the articular facets to both one-another, and to the overall anteroposterior length of the bone. With this caveat in mind, the height of the anterior articular surface is approximately 0.85 the height of the posterior surface, with the width of their articular facets being roughly subequal to their dorsoventral height. The anteroposterior length of the bone is approximately twice the dorsoventral height of the anterior surface and 1.82 times the height of the posterior end. Assuming that *Antetonitrus* displayed the same basic cervical proportions as most other non-eusauropodan sauropodomorphs (e.g., *Riojasaurus*; *Yunnanosaurus*; *Lessemsaurus*) then it is most likely that the centrum derives from somewhere towards the rear of the middle part of the neck.

The cervical centrum is strongly constricted mediolaterally, with its width at midlength less than half the width of the articular surfaces, although it is possible that depositional flattening has exaggerated this degree of constriction. The parapophyses are rugose longitudinal crests positioned just above mid-height on the anterior margin of the centrum. Dorsally, the neural-arch sutures are represented by two heavily rugose, anteroposteriorly flared parasaggital ridges extending the entire anteroposterior length of the bone and

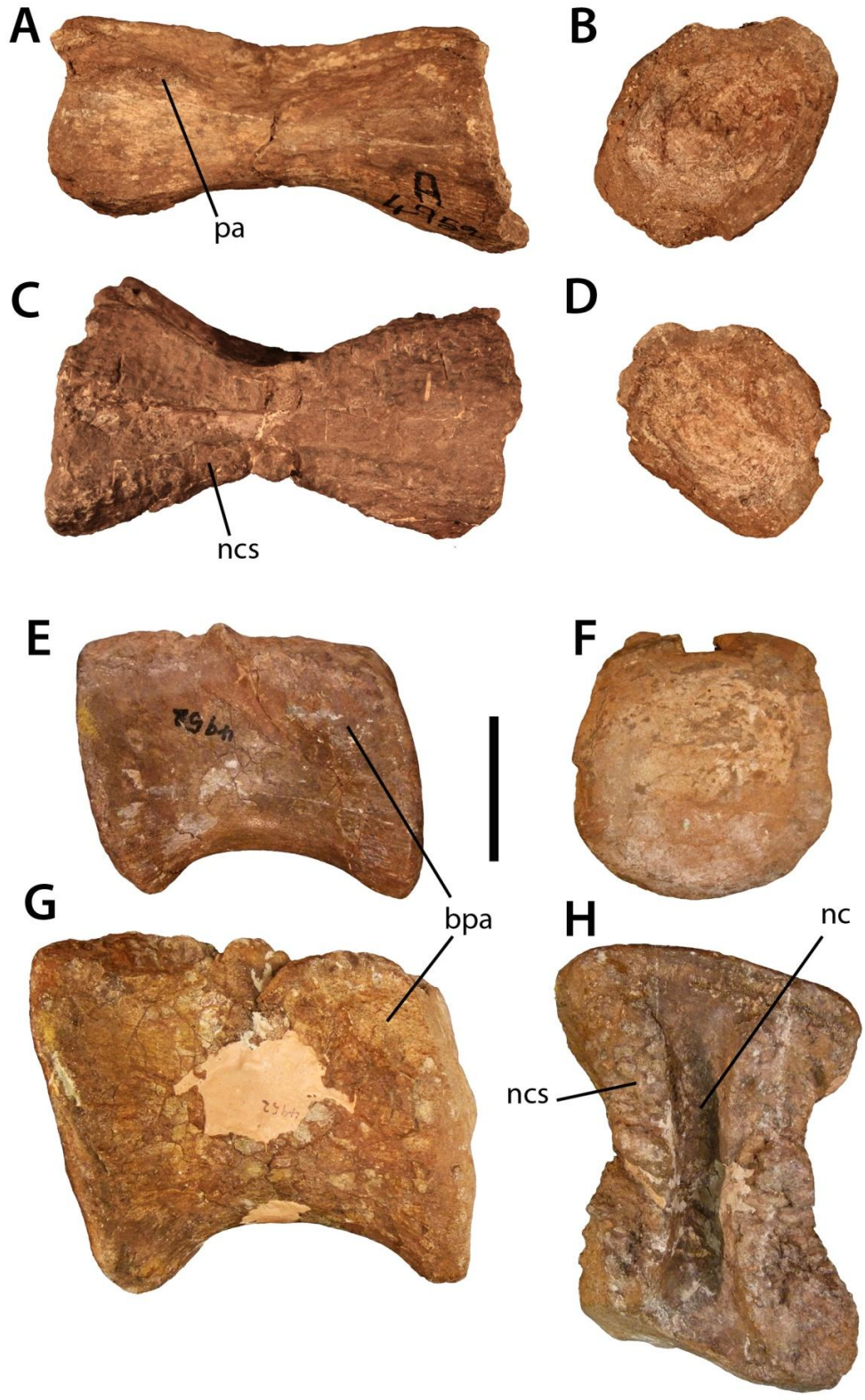

Fig. 3. *Antetonitrus ingenipes* (BP/1/4952), isolated centra. **A**-**D**: middle/posterior cervical centrum in **A**, left lateral; **B**, posterior; **C**, dorsal; **D**, anterior views. **E**-**F**: ?anterior dorsal centrum in **E**, right lateral; **F**, proximal views. **G**-**H**: ?mid-posterior dorsal centrum in **G**, right lateral; **H**, dorsal views. Abbreviations: bpa, base of parapophyses; nc, neural canal; ncs, neuro-centro suture; pa, parapophyses. Scale bar = 5cm

separated by a relatively deep neural canal (at least where it is not obscured by remaining matrix).

It is possible that a subtle ventral keel, observable in some non-eusauropodan taxa (e.g., *Massospondylus*; *Lamplughsaura; Isanosaurus*) was present on the anterior half of the ventral surface of the centrum, but it cannot be said with confidence whether or not this is an artefact of distortion.

4.1.2 DORSAL VERTEBRAE

General overview: There are four disarticulated neural arches and four centra (**Fig.3**) of the dorsal series present. Post-depositional distortion has warped most of the centra, thus making it difficult to establish whether they articulated with any of the preserved neural arches in life. This lack of dorsal fusion is indicative of an immature animal. All of the centra are amphicoelous and acamerate (solid). The anteroposterior length of the dorsal centra that have not experienced major dorsoventral compression is roughly subequal to the height of their posterior surfaces. This ratio is fairly typical for Sauropodomorpha whereas most massospondylids (e.g. *Massospondylus*; *Adeopapposaurus*) display an elongated length/height ratio of about 1.5 in the dorsal centra (Apaldetti et al. 2012).

Based on the position of the parapophyses, the vertebral elements range from the middle-anterior to the posterior-most segments of the dorsal column. The anterior most neural arch - possibly located somewhere between D4 and D6 - is the smallest of the dorsal neural arches, as is typical of anteriorly located dorsal vertebrae in sauropodomorphs. The next in the series probably represents a middle-to-mid-posterior neural arch and is hypothesised as being located somewhere between D8 and D10. The final two dorsal arches probably represent an identical position in the vertebral series (based on equivalence in morphology) as the posterior-most dorsal neural arches. As one is clearly smaller (as well as being less well preserved), it probable that at least two individuals are represented within the dorsal remains of the *Antetonitrus* vertebrae.

All of the disarticulated neural arches and centra interpreted as dorsal elements within the *Antetonitrus* assemblage display a similar relationship, with the former being roughly two to three times the dorsoventral height of the latter. This ratio, if it is correct, would represent a

marked departure from the general non-sauropodan sauropodomorph condition, where the neural arches of the dorsal series are sub-equal to slightly higher than the articular surfaces of the centra with which they connect (e.g., *Plateosaurus*; *Riojasaurus*; *Lufengosaurus*; *Yunnanosaurus; Leonerasaurus*). The putative ratio observed in *Antetonitrus* is closer to that of sauropodan taxa such as *Tazoudasurus* and *Shunosaurus* where the dorsal arches are two to three times the height of their centra.

Much of the great dorsoventral height of the neural arches is conferred by especially tall neural spines, which in the anterior-most neural arch constitutes 0.56 the total dorsoventral height of the bone. This represents another departure from the typical non-sauropodan sauropodomorph condition, in which the neural spine is half to less-than-half the total height of the anterior neural arches (e.g., *Plateosaurus*; *Massospondylus*; *Yunannosaurus*; *Jingshanosaurus*). The only known non-eusauropodan sauropodomorphs to also display similarly high neural spines are *Lessemsaurus*, *Tazoudasuaurus and Isanosaurus*, although in *Lessemsaurus* the neural spines are slightly lower at approximately 0.52 the total height of the arch. As in *Lessemsaurus,* the neural spines in *Antetonitrus* are transversely widened at their dorsal margin compared to most non-eusauropodan sauropomorphs (e.g. *Massospondylus*; *Anchisaurus*), although not to the degree seen in *Tazoudasaurus* + Eusauropoda.

The neural spines of all the dorsal elements are plesiomorphic insofar as they lack the pronounced anteroposterior constriction typical of *Tazoudasaurus* and eusauropodan genera, while also lacking the spinodiapophyseal laminae present in *Tazoudasaurus* and more derived sauropods. Furthermore, none of the dorsal vertebrae of *Antetonitrus* has the anterior centroparapophyseal lamina, intraprezygapophyseal lamina, or the prezygoparapophyseal lamina present in *Tazoudasaurus* and more derived sauropods.

The articular facets of the zygapohyses in all the preserved dorsal neural arches of *Antetonitrus* are completely flat (irrespective of angled orientation), lacking the concave curvature observed in some of the dorsal neural arches of *Coloradisaurus* (Apaldetti et al. 2012). In the mid-anterior dorsal neural arch the prezygapophyses are especially large relative to the size of the neural arch, with their joint mediolateral width 0.5 times the maximum width of the neural arch (across the transverse processes). In the two posterior

dorsal neural arches this metric is significantly reduced at about 0.39. Accordingly, throughout the dorsal vertebral sequence the transverse processes increase in relative width, being 0.73 times the total height of the neural spine in the mid-anterior neural arch and 1.04 in the posterior-most arch.

The neural canals of the dorsal neural arches are markedly high, slot-shaped channels with sub-vertical walls. This contrasts with the condition in most basal sauropodomorphs (e.g. *Plateosaurus*; *Eucnemesaurus*; *Massospondylus*; *Lamplughsaura*) that tend to have low, subcircular neural canals in the dorsal series. In posterior view, the hyposphenes of all the dorsal vertebrae of *Antetonitrus* are markedly well-developed equilateral triangles with ventral surfaces that are as mediolaterally broad (if not slightly more) as the neural canal. *Antetonitrus* was originally described as having hyposphenes as deep as the neural canals that they cap (Yates and Kitching 2003). However, this is clearly not the case in both the mid-anterior and mid-posterior neural arches, where the hyposphenes constitute only approximately 0.65 and 0.68 of the canal height, respectively. Nonetheless, the hyposphenes in *Antetonitrus* appear to represent a particularly robust variant of the state typical to most derived basal sauropodomorphs (e.g. *Massospondylus*; *Aardonyx*), whereas the hyposphenes of *Tazoudasurus* and most eusauropods are either mediolaterally attenuated or relatively reduced in sized.

In accord with the high neural canal, the pedicles of the dorsal neural arches in *Antetonitrus* are also dorsoventrally elongate, meaning that the prezygopophyses would have been raised well above the anterodorsal lip of the centrum, further contributing to the great relative dorsoventral height of the element. In contrast, most other non-eusauropodan sauropodomorphs (e.g. *Massospondylus*; *Lessemsaurus*) tend to have considerably lower dorsal neural arch pedicles.

The following description will focus on the major distinguishing characteristics of the three largest, most complete neural arches. These are hypothesised to have derived from a single individual.

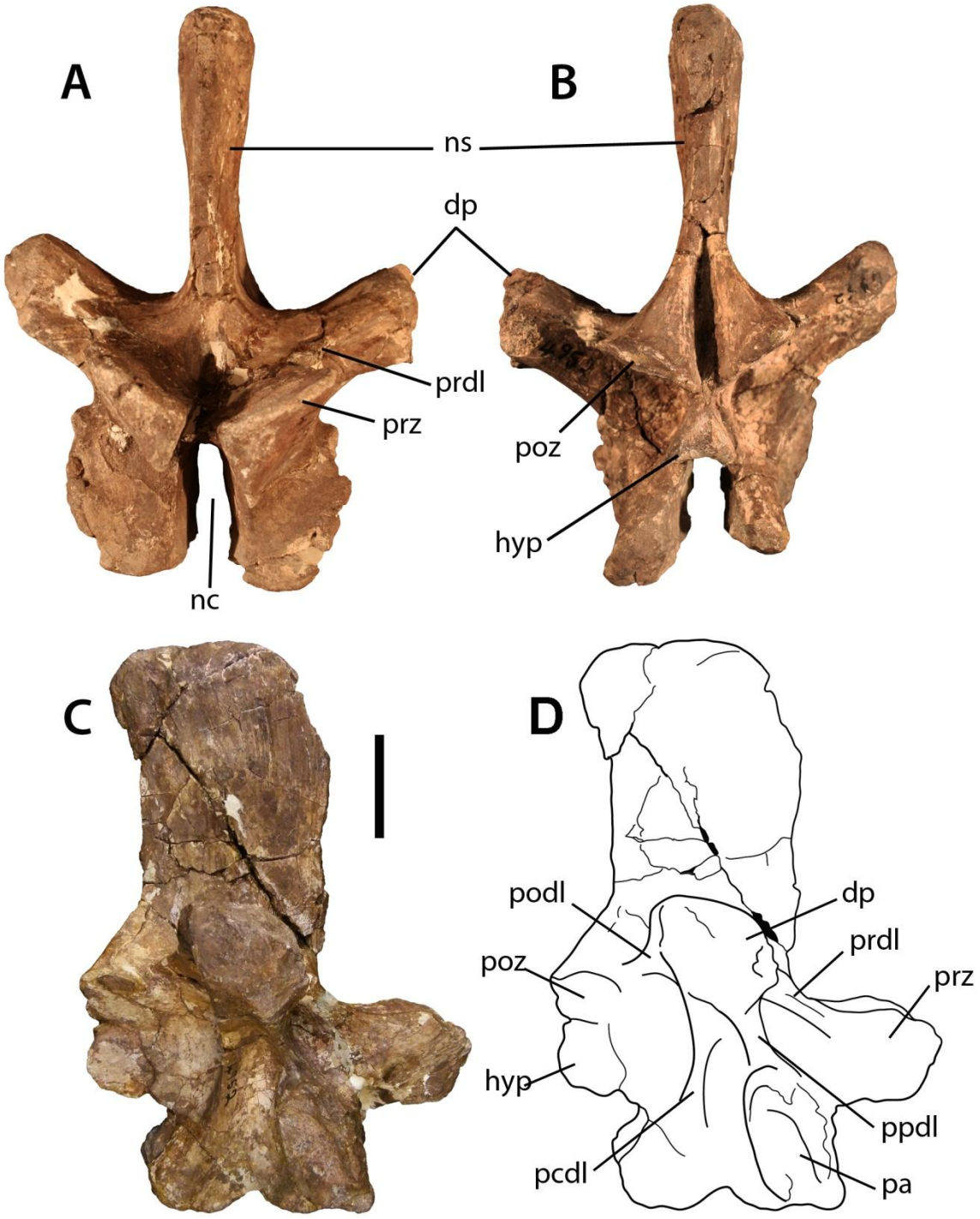

Fig. 4. *Antetonitrus ingenipes* (BP/1/4952)*,* mid-anterior dorsal neural arch in **A**, anterior; **B**, posterior; and **C**, **D**, lateral views. Abbreviations: dia, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; pcdl, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; poz, postzygapophyses; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prz, prezygapophyses. Scale bar = 5cm.

Mid-anterior dorsal neural arch: As in *Plateosauravus*, it is possible that the anterior margin of the neural spine of both the mid-anterior and mid-posterior neural arches possessed a 'keel' (possibly homologous with the prespinal laminae of later sauropods [Wilson 1999]); however, damage to both elements makes this difficult to verify and the process, if complete, is likely to have been relatively subtle. The neural spine of the mid-anterior neural arch is buttressed posteroventrally by incipient spinopostzygapophyseal laminae (spol) that exhibit a similar degree of development to that observed in derived basal sauropodomorphs (e.g. *Riojasaurus*; *Aardonyx*), but lack the flared, posterior expansion that braces most of the dorsoventral length of the neural spines in eusauropods (**Fig. 4**). Together, these bound a deep postspinal sulcus.

The postzygapophyseal facets are ovoid and directed medioventrally at an angle of about 40 degrees where they meet the apex of the hyposphene ventrally. The prezygapophyses are large subcircular processes (in dorsal aspect) separated medially by a well developed hypantrum and inclined at a similar angle as the postzygapophyses.

The transverse processes extend dorsolaterally and slightly posteriorly, rising above the level of both the posterior and anterior zygapophyses, as is typical of more anteriorly located dorsal vertebrae. The diapophyses are roughly pentagonal in lateral outline, mainly on account of the four primary saurischian vertebral laminae that radiate from their anterior, posterior and ventral margins (Wilson 1999). The postzygadiapohyseal lamina (podl) connects the diapophyses with the postzygapophyses via a stout, dorsally inclined strut. The posterior centrodiapophyseal lamina (pcdl) is the longest and thinnest of the laminae and extends from the diapophyses towards the posteroventral corner of the neural arch. The paradiapophyseal lamina (ppdl) is a short anteroventral extension linking the diapophyses with the parapohyses, the latter of which appear to have risen completely above the level of the centrum, thus occupying the entire anteroventral corner of the bone. The prezygadiapophyseal lamina (prdl) extends anteriorly at a slight ventral incline to connect the diapophyses with the prezygapophyses.

The neural arch of the mid-anterior dorsal vertebra in *Antetonitrus* is acamarate as in most non-eusauropodan sauropodomorphs (Galton and Upchurch 2004). The fossa bounded by the podl and the pcdl (posterior infradiapophyseal fossa *sensu* Yates et al. 2012) extends

deeply into the arch, terminating roughly level with the anterior margin of the diapophyses, although without any bone invasion (or sub-fossae) being present.

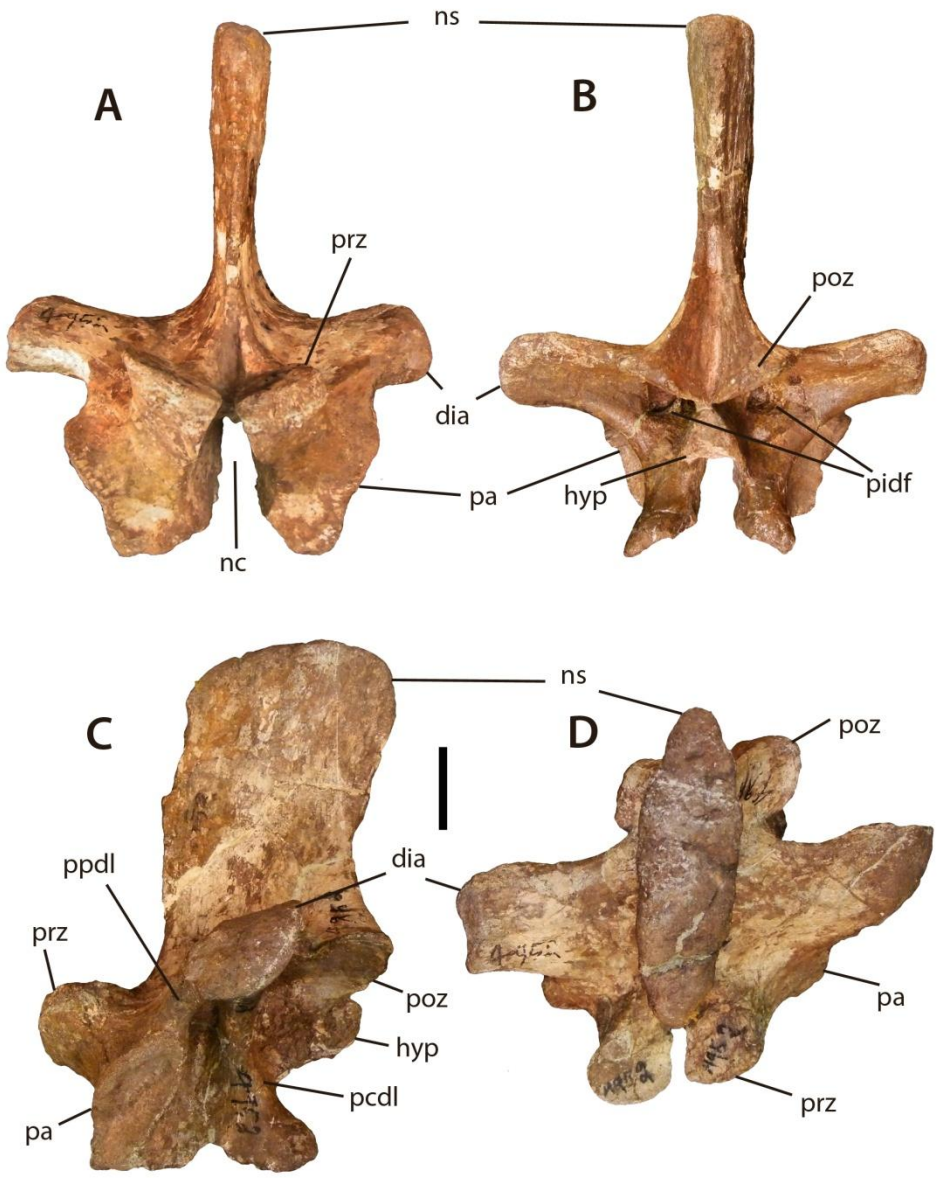

Fig.5. *Antetonitrus ingenipes,* mid-posterior dorsal neural arch (BP/1/4952) in **A**, anterior; **B**, posterior; **C**, lateral; **D**, dorsal views. Abbreviations: dia, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; pidf, posterior infradiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; poz, postzygapophyses; ppdl, paradiapophyseal lamina; prz, prezygapophyses. Scale bar = 5cm.

Middle-posterior neural arch: The neural spine of the mid-posterior dorsal arch presents the same basic proportions as in the more anterior dorsal neural arch (**Fig. 5**). The dorsoventral height of the neural spine is approximately 0.56 of the total height of the neural arch, whereas the height of the neural spine is roughly 1.5 times the anteroposterior length of its

base. This latter ratio is relatively high for a non-eusauropodan sauropodomorph, being greater than the same ratio in both *Melanorosaurus* and *Lessemsaurus* (1.3 – 1.47 in the mid-dorsals of PVL 4822). The condition in *Antetonitrus* recalls that of derived sauropodan taxa (e.g. *Tazoudasurus*; *Mamenchisaurus*) in which the middle dorsal neural spines are markedly dorsoventrally elongate. However, the neural spine in *Antetonitrus* retains the expansive anteroposterior length common to non-sauropodan sauropodomorphs.

In both the mid-anterior and mid-posterior neural arches the neural spine is oriented somewhat posteriorly, with a subtle bow-like curvature of the anterior margin. This differs from the (more plesiomorphic) condition observed in *Lessemsaurus* in which the dorsal neural spines project anterodorsally along their anterior margin, so that the dorsal surfaces of the spines are anteroposteriorly expanded relative to their base. The spol in the mid-posterior dorsal arch displays a similar degree of development as that observed in the mid-anterior dorsal arch.

Relative to the mid-anterior neural arch the zygapophyses are set at a slightly reduced angle of about 30 degrees from the horizontal. As is typical of basal Sauropodomorpha, the prdl is no longer present by this point in the vertebral series, likely having been lost somewhere in the transition between the anterior-to-middle dorsal vertebrae. The ppdl and pcdl are still clearly expressed, being both shorter and more robust than in the mid-anterior dorsal arch. The mid-posterior neural arch also displays incipient spinoprezygapophyseal laminae which bound a relatively deep prespinal sulcus, a feature shared with *Lessemsaurus*, but seen to a lesser degree in a number of non-sauropodan taxa (e.g., *Plateosauravus*; *Massospondylus*; *Aardonyx*).

The transverse processes of both posterior dorsal vertebrae of *Antetonitrus* are completely horizontal, as in all non-eusauropodan sauropodomorphs (Pol et al. 2011). The orientation of the concave parapophyses in the mid-posterior neural arch is similar to that of the mid-anterior arch, extending posterodorsally as oblique ellipsoid crests. Furthermore, as in the mid-anterior neural arch, the parapophyses are positioned only marginally anterior to the diapophyses. This condition is quite different from the morphology observed in the middle-to-posterior dorsal vertebrae of *Lessemsaurus* and most other non-sauropodan taxa (e.g. *Plateosaurus*; *Massospondylus*; *Yunnanosaurus*) where the parapophyses are set much

further forward from the diapophyses than in *Antetonitrus*. In a number of basal sauropodomorph taxa (e.g. *Massospondylus; Lufengosaurus; Lessemsaurus*) this results in a pronounced, wing-like laminar shelf that runs almost horizontally between the parapophyses and the diapophyses (the ppdl), a condition that is absent in all known dorsal neural arches of *Antetonitrus.*

Perhaps the most important distinguishing feature of the mid-posterior neural arch in *Antetonitrus* is the presence of well-developed pneumatic subfossae that penetrate the posterior infradiapophyseal fossae on both sides. These were recently described in detail by Yates et al. (2012). Similar – albeit far less developed – pneumatic structures are only currently known from the dorsal vertebrae of *Eucenemsaurus* and *Aardonyx* outside of Eusauropoda (although it is possible that a posterior dorsal in *Tazoudasaurus* exhibited similar subfossae [Allain and Aquesbi 2008: Text Fig. 14]).

Posterior-most dorsal neural arch: The neural spine of the posterior-most neural arch (possibly the last non-sacral vertebra) is straighter, shorter anteroposteriorly, and more expanded transversely than the two more anterior dorsal arches (**Fig.6**). This element appears to have had relatively well-developed spinopostzygapophyseal laminae that extended for over half the dorsoventral height of the neural spine. However, as this element was damaged during a post-preparation casting attempt, the original figure from Yates and Kitching (2003: fig. 3) stands as the only complete record. The spol frame an expansive area on the posterior surface of the neural spine that is both flatter and mediolaterally broader than the slit-shaped postspinal sulci of the two more anterior dorsal neural arches. Similarly, the anterior surface of the posterior-most neural spine is also mediolaterally expanded, lacking the incipient spinoprezygapophyseal laminae of the more anterior dorsal arches. This broad, flattened area dorsal to base of the prezygapophyses is divided down the middle by a pronounced prespinal ridge (= ?lamina), as opposed to the more typical prespinal sulci of the more anterior neural arches. This ridge merges with the anterior margin of the neural spine as a broad keel which is less ambiguous in definition than in the two more anterior dorsal neural arches.

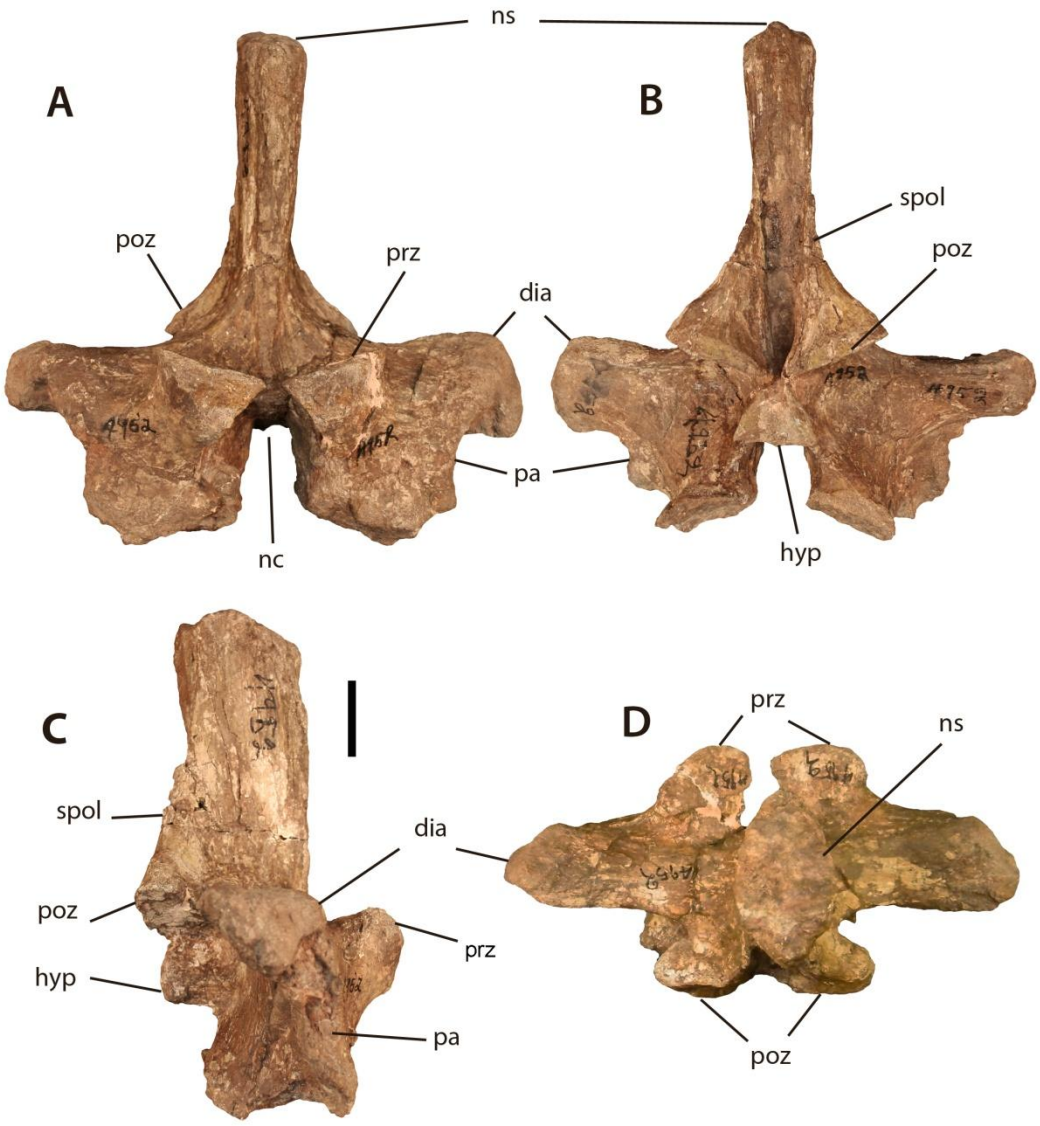

Fig.6. *Antetonitrus ingenipes,* posterior dorsal nueral arch (BP/1/4952) in **A**, anterior; **B**, posterior; **C**, lateral; **D**, dorsal views. Abbreviations: dia, diapophyses; hyp, hyposphene; nc, neural canal; ns, neural spine; pa, parapophyses; poz, postzygapophyses; prz, prezygapophyses; spol, spinopostzygapophyseal lamina. Scale bar = 5cm.

The prezygapophyses are smaller and less anteriorly projecting than in the two more anterior arches, with both the zygapophyseal articular facets reduced to an angle of <30 degrees. Compared to the more anterior dorsal neural arches, the dorsoventral height of the transverse processes of the posterior-most neural arch is considerably greater than their anteroposterior length. This is expressed throughout the element, with the vertebral arch anteroposteriorly compressed in such a fashion that no single lamina is particularly pronounced (with the exception of the spol). However, highly reduced pcdl can still be

discerned, as can broad, shelf-like podl. This anteroposterior compression presages the condition common to sacral vertebrae.

The parapophyses are present as ventrally-directed ellipsoid concavities that essentially excavate the anteroventral surface of the diapophyses. The parapophyseal rim is emarginated to a similar – if not slightly more developed – degree as in the parapophyses of the mid-posterior dorsal vertebra. It is possible that this morphology presages the hollowed-out attachments for the ball-like sacral-ribs of the sacrum; however, as in vertebrae immediately anterior to the sacrum, this element may have been ribless (Nair, pers. comm.; see also von Huene 1926: Plate II, Fig. 3).

The hyposphene is subequal in depth to the neural canal only in the posterior-most arch. It also possesses a distinct medial ridge beginning in the middle its posterior surface that extends along the ventral surface for most of its length. The mid-posterior arch displays a similar medial bump on the ventral surface of the hyposphene, but this not as distinct a crest as in the more posterior arch.

4.1.3 ?CAUDOSACRAL/ANTERIOR CAUDAL

There is an isolated neural arch (**Fig. 7**) that was originally allocated to the sacrum (Yates and Kitching 2003). However, as both the centrum and the transverse processes/sacral ribs are missing, it is possible that it represents an anterior caudal neural arch. Some features, however, suggest that this neural arch belongs to the sacrum, possibly as a caudosacral, and these will be discussed below.

The neural spine is remarkably tall and transversely thin, being 2.3 times higher than the length of its base and over two thirds the height of the entire arch. The neural spine rises dorsally with a gentle posterior bowing that contrasts with the uniformly oblique angle observed in the caudal vertebrae. Where present, the caudosacrals of other sauropodomorph taxa (i.e. *Plateosaurus*; *Melanorosaurus* [NM QR 1551]) are similarly arcuate, if lacking the marked dorsoventral height observed in *Antetonitrus*. The anterior margin of the neural spine appears to have had a subtle keel similar to that of the two more anterior dorsal neural arches. On the left side of the neural spine this anterior keel is demarcated by a distinct groove or sulcus that is visible along the entire dorsoventral extent

of the neural spine. However, it is possible that this groove may have been exaggerated during preparation. The posterior surface of the neural spine is divided by thin, sheet-like spinopostzygapophyseal laminae that may have extended for most of the dorsoventral height of the spine, although poor preservation at the posterodorsal margin makes this difficult to confirm. This lamination is clearly absent from all the other caudal elements within the assemblage. In contrast, the postzygapophyses that form the base of the spol are reduced and steeply angled (c. 70˚) as is typical of caudal vertebrae.

Ventral to the postzygapophyses there is a thin but dorsoventrally tall hyposphene. The presence of hyposphenes on proximal caudals/caudosacrals is a complexly distributed character throughout Sauropodomorpha. The presence of a hyposphene has been regarded as a synapomorphy of *Vulcanodon* + Sauropoda in the past (Upchurch 1998; Yates et al. 2004). However, there is reason to suspect that the distribution of caudal hyposphenal ridges was not restricted to Sauropoda *senso stricto*, as a number of undescribed (and unaccessioned) proximal caudal elements from the Los Colorados Formation housed in the collections of the Institutio Miguel Lillio display hyposphenal ridges. Additionally, a small hyposphene is observable in a partial ?anterior caudal/caudosacral neural arch located amongst material informally referred to *Aardonyx* (BP/1/386), and a hyposphenal ridge has also been cited in specimens of *Melanorosaurus* (Yates 2007a,b). A hyposphene on either the caudosacral or anterior-most caudal vertebra is subsequently regarded as a tentative apomorphy of *Antetonitrus* here.

The prezygapophyses display the general caudal condition of being strongly anteriorly projected with elliptical facets set at an angle of about 70 degrees from the horizontal (in anterior aspect). They are connected to the neural spine via well-developed spinoprezygapophyseal laminae. The prezygapophyseal facets have an ossified lip of bone that is clearly visible along their medioventral edge. This lip of bone would have provided an additional cradling mechanism for the hyposphene of the vertebra immediately anterior to it (= ?second primordial), and may potentially relate to the general strengthening of the sacral unit.

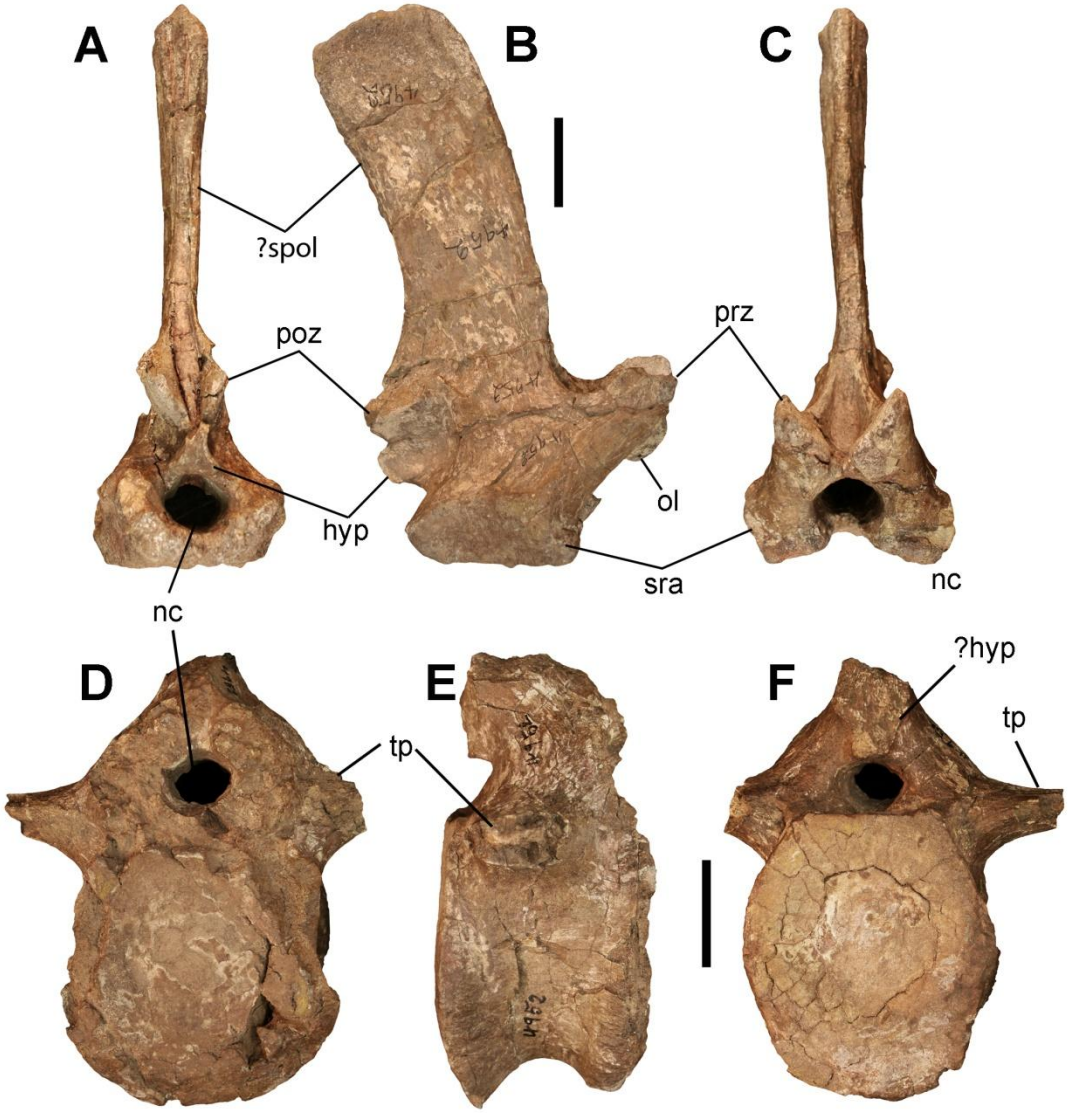

Fig. 7. *Antetonitrus ingenipes*. **A**-**C**: ?caudosacral neural arch (BP/1/4952) in **A**, posterior; **B**, lateral; **C**, anterior views. **D**-**F**: anterior caudal vertebra (?BP/1/4952b) in **D**, anterior; **E**, lateral; **F**, posterior views. Abbreviations: nc, neural canal; hyp, hyposphene; ol, ossified lip; poz, postzygapophyses; prz, prezygapophyses; spol, spinopostzygapophyseal lamina; sra, possible sacral rib articular surface; tp, transverse process. Scale bar = 5cm

As in the rest of the caudal series the neural canal is short and circular in cross section, lacking the pronounced dorsoventral expansion of the dorsal neural arches. Evidence that this neural arch articulated with the ilium as part of the sacral unit can be seen in the steeply inclined suture scars at the base of the arch. Many of the caudal vertebrae within the *Antetonitrus* assemblage are missing the transverse process; however, all are broken and/or snapped in a manner that one would expect from general post-depositional stresses,

with no evidence of fusion-lines. In contrast, the base of the neural arch described here displays the rugose, slightly concave surface reminiscent of the sacral rib articular surfaces seen in the disarticulated neural arches of other sauropodomorphs (e.g. *Lamplughsaura*; referred specimen of *Antetonitrus* [BP/1/5091]). This un-fused surface is much lower than the wing-like projections typical of the neural arches in primordial sacral vertebrae, being anterposteriorly longer than high. The rugose concavity is bordered dorsally and posteriorly by a slight emargination.

In light of the above discussion this element is best interpreted as the posterior-most sacral vertebra or the anterior-most caudal vertebra which may have joined the sacrum as a caudosacral. This raises the possibility that *Antetonitrus* displayed at least four sacral vertebrae (assuming the additional presence of the typical dorsosacral) as in *Leonerasaurus* and *Melanorosaurus* + *Sauropoda* and further corroborates the phylegenetic scenario outlined in Pol et al. (2011) in which a four vertebrae sacrum represents a synapomorphy of the above taxa.

4.1.4 CAUDAL VERTEBRAE

There are twelve caudal vertebrae present. Based on relative proportions it is likely that the majority (ten) belong to a larger individual, while at least two are from a smaller, possibly juvenile individual. A mid-anterior caudal (**Fig. 8**) from the smaller specimen is the only fully complete caudal vertebra present and will therefore form the main focus of the following description, although changes throughout the series will also be addressed.

The caudal vertebrae of *Antetonitrus* are broadly typical all of non-eusauropodan sauropodomorphs. All of the caudal centra within the assemblage are shallowly amphicoelous and constricted mediolaterally with a deeply concave (when viewed laterally) ventral surface. As in all non-eusauropodan sauropodomorphs the neural arch (where preserved) occupies the majority of the anteroposterior length of the centrum, being generally confluent with the anterior face of the centrum, and set slightly forward from the posterior face. The ventral surfaces of the articular faces of all caudal centra display the characteristically thickened lip that represents the oblique articular facets for the chevrons. This is generally most developed on the posteroventral surface, which is interesting given

that none of the preserved chevrons display a clear proximo-anterior facet – the facet that would have articulated with the posteroventral surfaces of the caudal centra.

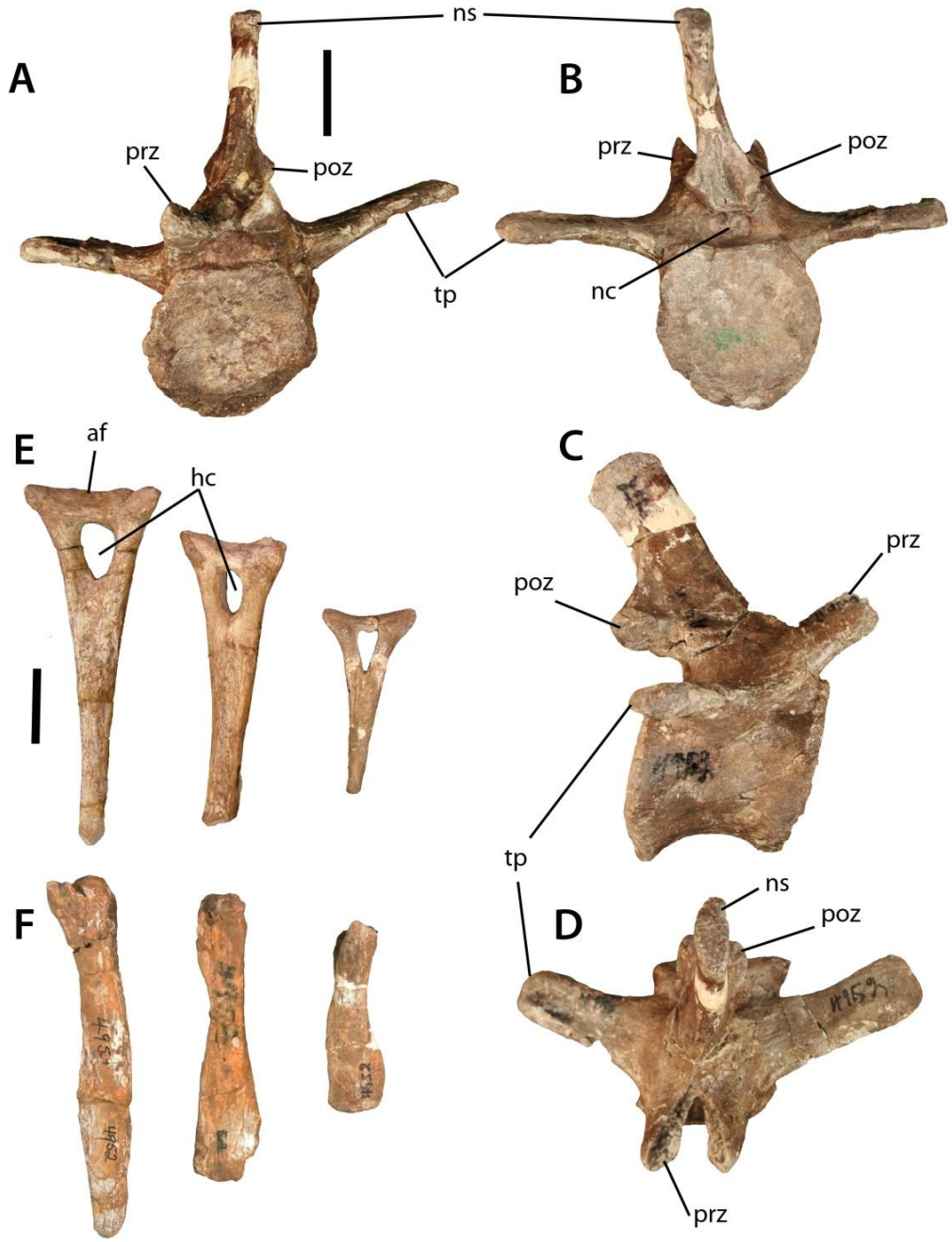

Fig. 8. *Antetonitrus ingenipes*. **A**-**D**: mid-caudal vertebra (small individual: BP/1/4952b) in **A**, anterior; **B**, posterior; **C**, lateral and **D**, dorsal views. **E**-**F**: Chevrons (BP/1/4952) in **E**, posterior and **F**, lateral views. Abbreviations: af, articular facet; hc, haemal canal; nc, neural canal; ns, neural spine; poz, postzygapophyses; prz, prezygapophyses; tp, transverse process. Scale bar = 5cm.

An anterior caudal vertebra (also possibly from the smaller individual) that is missing both its transverse processes and neural spine represents the most anterior caudal, though its precise position is unknown (**Fig. 7**). As is typical of anterior caudal vertebrae in derived sauropodomorphs (e.g. *Lufengosaurus*; *Aardonyx*) the centrum is much higher than long, with its anteroposterior length 0.66 times its dorsoventral height. The articular faces are slightly ovoid, being higher than transversely wide, with neither surface offset relative to the other. This element fails to display the ventral excavation of the anterior caudal centrum described for *Vulcanodon* and an unnamed sauropod from the Upper Elliot formation (BP/1/6105: possibly referable to *Vulcanodon*) (Yates et al. 2004). As in those specimens it is possible that the anterior-most caudal vertebra of *Antetonitrus* may have possesed a hyposphenal ridge, although breakage to the neural arch prior to the level of the postzygapophyses makes this impossible to confirm.

In the fully complete mid-anterior caudal the transverse processes extend posterolaterally with a slight dorsal elevation, becoming increasingly posteriorly swept-back in more posterior vertebrae. The transverse processes in this element are long, being only slightly shorter than the neural spine. There is a moderately deep fossa beneath the buttress connecting the transverse processes to the prezygapophyses, a feature that can also be seen in a mid-anterior caudal vertebra of *Aardonyx*, but cannot be distinguished in any other of the *Antetonitrus* caudals. The prezygapopheses project well forward from the anterodorsal margin of the centrum; their articular facets are elongate and set at angle of about 50 degrees. There is no spinoprezygapophyseal laminae present, although an incipient keel is visible on the ventral margin of the anterior surface of the neural spine. The postzygapophyses are set at a slightly steeper angle than the prezygapophyses, and also lack clear laminae. The neural spine is relatively deep, being approximately three-quarters the anteroposterior length of the base of the neural arch. Neural spines of anterior caudal vertebrae that are greater than half the length of their associated neural arch has been cited on more than one occasion as a synapomorphy of sauropodomorphs basal to Sauropoda (i.e. 'Prosauropoda') (Yates 2003a; Upchurch 2007b). However, the cogency of this character is questioned here because several basal (and not so basal) sauropods (e.g., *Tazoudasaurus*; *Shunosaurus*; *Barapasaurus)* display anterior neural spines that are clearly over half the anteroposterior length of the neural arch – although it is not clear if 'neural

arch length' is intended as meaning between the zygapophyses or along the contact-line with the centrum (although it would appear that the above still applies even in the case of the former, see Zhang 1988; Allain and Aquesbi 2008: Text-Fig. 16; see also below: 'Cladistic Analysis'). The neural spine of the complete mid-anterior caudal is minimally transversely expanded and directed posteriorly at an angle of about 50 degrees.

The articular facets of the caudal centra become progressively more circular in posterior elements of the series. This is accompanied by a general lengthening of the centrum relative to its height, with the neural arch positioned slightly more anteriorly from the mid-caudals onwards. Towards the posterior end of the series the transverse arches become progressively more posteriorly sweptback, being ultimately reduced to low ridges on the lateral sides of the centrum in the posterior-most caudals. Likewise, the neural spine becomes progressively posteriorly located, disappearing entirely in the posterior-most elements. These changes can be observed in the caudal series of most sauropodomorph taxa (e.g. *Lufengosaurus*, *Yunnanosaurus*).

4.1.5 CHEVRONS AND RIBS

There are two dorsal ribs present. Although they are preserved together in close proximity and lying parallel to one another, their distal and proximal ends are juxtaposed – indicating the degree of taphonomic displacement the *Antetonitrus* assemblage experienced prior to fossilization. Both ribs have long, curved shafts, although only one completely preserves the capitulum and tuberculum, which are typically diapsidan in appearance. There is the partial shaft of a third rib obliquely overlying these two elements.

There are several isolated chevrons of typical non-eusauropodan morphology (**Fig. 8**). The proximal end forms the distinctive Y shape whereupon it is transversely bridged by the posterodorsally concave inter-centrum facet. Unlike a number of derived sauropodomorphs that appear to have possessed an additional facet on the anterior margin of the proximal surface for articulation with the caudal centra (e.g. *Lamplughsaura*; *Aardonyx*; *Tazoudasaurus*), *Antetonitrus* presents but one large posterodorsal facet. Distal to this facet is the prominent, triangular foramen (=haemal canal) for the caudal blood vessels (Cooper 1984).

In all preserved chevrons the distal blade is mediolaterally compressed, however, the distal end of the blade in more posterior-located chevrons becomes increasingly truncated and anteroposteriorly expanded, potentially presaging the distally forked chevrons of later sauropodan taxa (although a similar distal expansion is observable in other non-eusauropodan sauropodomorphs [e.g., *Plateosaurus*]).

4.2 APPENDICULAR SKELETON

Note on the pectoral girdle and forelimb: The scapula and forelimb of Antetonitrus *were described in some detail as minor component of a larger unpublished PhD thesis by Remes (2008). However, Remes was primarily concerned with changes in the myology and functional anatomy of the forelimb during the early evolutionary history of Sauropodomorpha (as opposed to a detailed comparative osteological/taxonomic account of the* Antetonitrus *assemblage). His descriptions are therefore rather brief (especially those pertaining to the ante-brachium and manus), while an idiosyncratic use of orientation terminology – designed to reflect the precise orientation of the bones in life – can make the descriptions difficult to follow at times. Remes nonetheless made several interesting observations, and these will be cited appropriately within the following descriptions.*

4.2.1 SCAPULA

There are three scapulae present, all belonging to separate individuals. In accord with the revised diagnosis (see above), these scapulae are hereafter referred to as BP/1/4952 (a large left), BP/1/4952b (a small right), and BP/1/4952c (another left, slightly smaller in dimension to BP/1/4952). As BP/1/4952b is missing a portion of its anteroventral corner, BP/1/4952 and BP/1/4952c will therefore form the main focus of the following description (**Fig.9**).

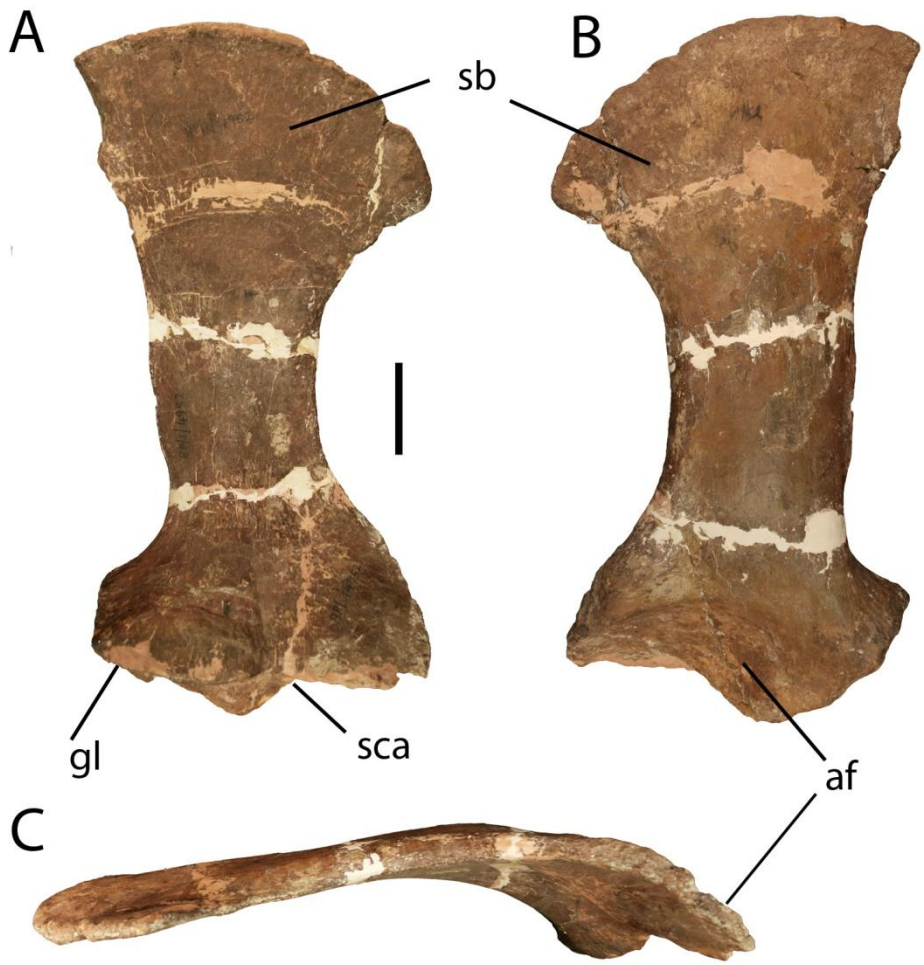

Fig. 9. *Antetonitrus ingenipes*, left scapula (BP/1/4952c) in **A**, medial; **B**, lateral; **C**, anterior views. Abbreviations: af, acromion facet; gl, glenoid; sb, scapular blade; sca, scapular-coracoid articulation. Scale bar = 10cm.

The scapula of *Antetonitrus ingenipes* is notably similar to that of *Lessemsaurus sauropoides* (PVL 4822/51: Pol and Powell 2007). As mentioned in the material and methods section, *contra* to Remes (2008) and in the aim of terminological simplicity, we assume an orientation where the distal end (free end) of the scapula is directed dorsally, where the acromial end of the scapula is directed ventrally, and where the surface of the scapula closest to the ribs is medial. As in *Lessemsaurus* both the ventral and dorsal ends are strongly expanded. The anteroposterior expansion of the dorsal end is 0.54 of total scapular length while the ventral end is slightly less expanded at 0.50. These proportions are almost identical to the same measurements in *Lessemsaurus*. As mentioned by Pol and Powell (2007:27) the vast majority of basal sauropodomorphs (e.g., *Plateosaurus*; *Massospondylus; Lufengosaurus; Coloradisaurus; Anchisaurus)* lack this pronounced expansion of the dorsal

end of the scapular blade, and certainly do not display scapulae in which the dorsal expansion is greater than that of the ventral. However, species such as *Riojasurus, Yunnanosaurus* and (possibly) *Gongxianosaurus*, while presenting a ratio of dorsal expansion to total scapular length that is lower than that of *Antetonitrus* and *Lessemsaurus*, still exhibit a relatively strong dorsal expansion with respect to the ventral end of the scapula. Interestingly, the majority of sauropodan taxa (e.g., *Isanosaurus*; *Shunosaurus*) present relatively attenuated scapular blades when compared with the condition observed in *Antetonitrus* and *Lessemsaurus*.

The ventral portion of the lateral surface is concave due to the deep acromion facet. This process occupies most of the lateral surface of the anteroposteriorly expanded ventral portion of the scapula, stretching as an ovoid fossa from the broken clavicular facet (possibly present in the largest left scapula [BP/1/4952] as a slight widening of the anterodorsal margin of the acromion, but this also is obscured by poor preservation) to just anterior of the glenoid region. The acromion facet is not bounded anterodorsally by an acromial ridge, and in this respect the scapula of *Antetonitrus* is more similar to non-eusauropodan sauropodomorphs than to more derived neosauropods which bear this feature (Upchurch et al. 2004). The anteroventral margin (= coracoidal suture) of the acromion facet is markedly thin whereas it thickens dramatically in the posterior half, being thickest at the distinct 'step' where the coracoidal articular surface meets the glenoid facet. As noted by Remes (2008) the scapulocracoidal articular surface possesses a ventrally extending lateral lip. A similar ventrolateral lip can be seen in the scapula of *Melanorosaurus* (NM QR1551). Both the glenoid and the coracoidal articular surfaces are strongly rugose.

Anteriorly, the medial surface of the ventral scapula is gently convex, while the posterior side of the medial surface rises as a pronounced convex ridge that runs from the coracoidal articular suture to a point about a third of the way along the ventromedial length of the shaft. According to the myological reconstruction of Remes (2008), this ridge delimits the facet for the M. subscapularis anteriorly, and the smaller facet for the M. serratus superficialis posteriorly. A similar ridge can be seen in most sauropodomorph taxa. The long axis (anteroposterior) of the ventral expansion and the long axis of the scapular blade form an angle of about 70 degrees, with the scapular blade angled slightly anteriorly relative to the ventral end. This angle is slightly reduced compared to the perpendicular angle present

in most basal sauropodomorphs, but still shy of the substantially reduced angle (c. 40 - 50 degrees) exhibited by some sauropodan taxa (e.g., *Spinophorosaurus*; *Barapasaurus; Omeisaurus*).

The minimum anteroposterior width at midshaft of the scapular blade of *Antetonitrus* is approximately 0.23 of total length, extremely similar to that of *Lessemsaurus*. As mentioned by Pol and Powell (2007:227), most sauropodomorphs have narrower scapular shafts with ratios varying between 0.15-0.17. This is true for both *Melanorosaurus* (0.17: NM QR 1551) and for a number of basal sauropod taxa including *Isanosaurus* and *Shunosaurus*. It is possible that *Gonxianosaurus* (He et al. 2008) may have displayed a broadened scapular shaft relative to total length, but an updated description of this poorly known taxon is required to confirm the presence or absence of this character. On the posterior margin of the scapular shaft there is a slight caudal flange that is associated with the facet for the M. serratus superficialis medially (Remes 2008).

The dorsal surface of the scapular blade is thin, planar and presents the typical convex outline in both medial and lateral views. As in *Lessemsaurus*, the largest scapula of *Antetonitrus* (BP/1/4952; broken in the other two elements) displays an acute flange on the posterior edge of the dorsal blade that exceeds the posteroventral corner of the ventral end in posterior expansion. This flange, along with the pronounced general expansion of the dorsal blade, means that both the anterior and (to a lesser degree) the posterior margins of the scapular blade in *Antetonitrus* are strongly concave.

4.2.2 HUMERUS

There are two right humeri; the larger (BP/1/4952) is nearly complete but is missing most of the radial condyle. The proximal half of the deltopectoral crest of the smaller humerus (BP/1/4952b) is damaged and the distal condyles – although complete – are flattened in a manner similar to the humeral head. The resulting effect is that the axis of both the distal and proximal (including the deltopectoral crest) halves of the smaller humerus lie in much the same plane. It is difficult to confidently associate either humerus with any of the scapulae. The length of the largest humerus is approx. 0.93 the length of the largest scapula (BP/1/4952). This ratio is relatively high for sauropodomorphs, although personal

observation of post-cranial material collected under *Melanorosaurus readi* (NM QR 1551) suggests a similar relationship between scapula and humerus in that taxon, and the newly described *Seitaad ruessi* (UMNH VP 18040: Sertich and Loewen 2010) may also have potentially displayed similar proportions (however, UMNH VP 18040 remains partially obscured by matrix). The length of the smaller right humerus is 0.78 the length of the smallest scapula (also from the right side), a proportion comparable to most derived sauropodomorphs (i.e., *Lunfengosaurus; Yunnanosaurus; Shunosaurus).* The larger humerus will provide the main focus for the following description (**Fig. 10**).

The proximal half of the bone is sub-rectangular in lateral view and is offset about 45 degrees from the transverse axis of the distal condyles, although this approaches almost 90 degrees at the apex of the deltopectoral crest. In this regard the humerus of *Antetonitrus* retains the plesiomorphic morphology of basal sauropodomorph taxa such as *Plateosaurus*, *Lufengosaurus* and *Massospondylus* which also display a similarly strong axial twist of the humeral shaft. In contrast, a number of other non-eusauropodan sauropodomorphs (i.e. *Lessemsaurus; Vulcanodon; Tazoudasaurus*) display a reduced axial twist, hence the roughly symmetrical "hourglass" morphology of the humerus of these taxa viewed in anterior aspect. However, Yates (2003a) and Remes (2008) have cautioned that the relative orientation of the deltopectoral crest (and hence the full degree of axial twist) is susceptible to geo-morphological processes, and is therefore not a good indicator of either phylogeny or function. The markedly different orientation of the deltopectoral crests exhibited by the two humeri in the *Antetonitrus* assemblage is emblematic of this phenomenon.
The transverse width of the distal portion of the humerus is approximately 0.30 times the total length of the bone, whereas the oblique anteroposterior expansion of the proximal half is 0.46 of total humeral length. These proportions are similar to most derived sauropodomorphs, however, *Lessemsaurus* and *Yunnanosaurus* are notable for having distally expanded condyles exceeding 0.4 times total humeral length.

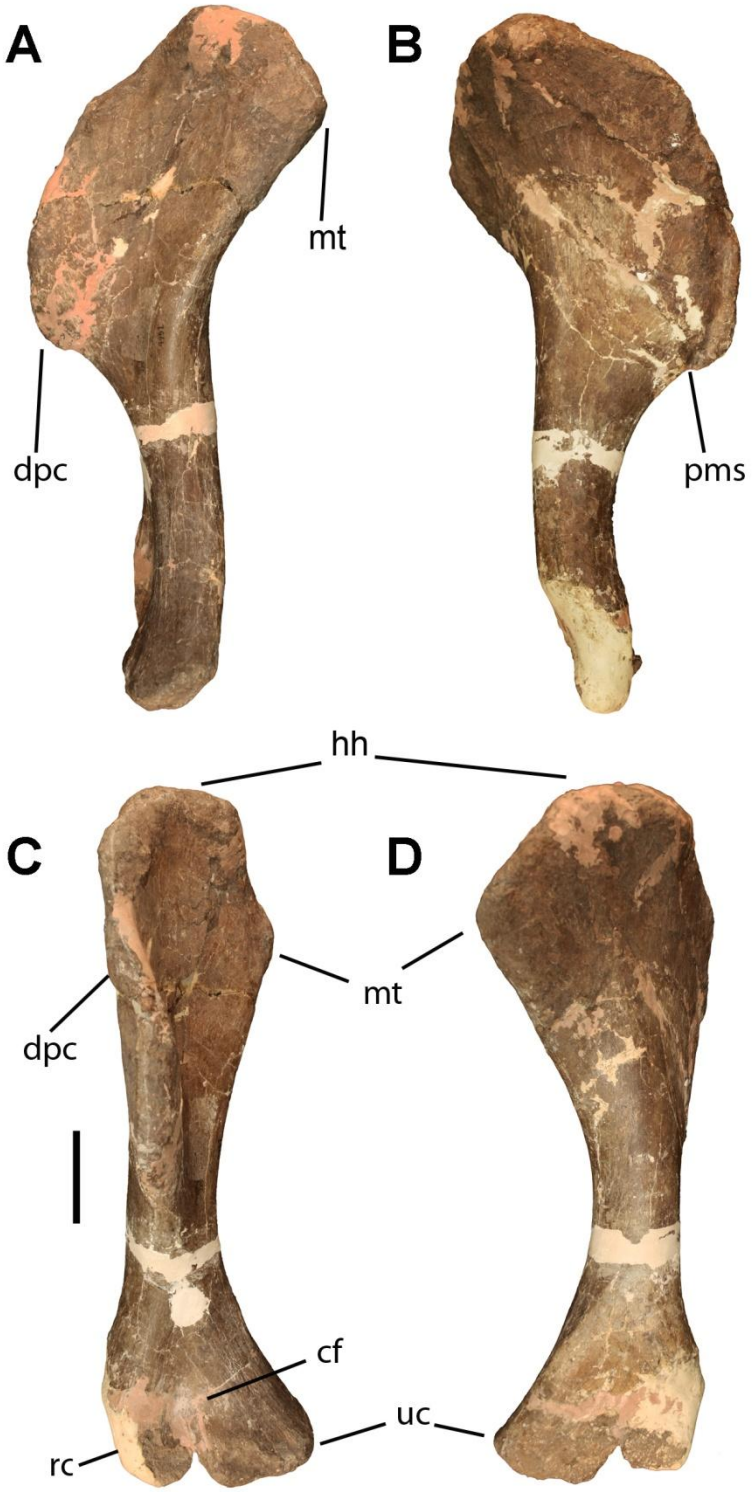

Fig. 10. *Antetonitrus ingenipes*, right humerus (BP/1/4952) in **A**, medial; **B**, lateral; **C**, anterior; **D**, posterior views. Abbreviations: cf, cuboid fossa; dpc, deltopectoral crest; hh, humeral head; mt, medial tuberosity; pms, para-marginal sulcus; rc, radial condyle; uc, ulnar condyle. Scale bar = 10cm.

Proximally, the head of the humerus is strongly convex, displaying the vaulted morphology characteristic of all suropodomorphs more advanced than the Plateosauridae (= Massopoda *sensu* Yates 2007a, b). The transverse width of the humeral head is thickest at the point where it would have articulated with the glenoid, after which it tapers posteromedially to form a sharp angle with the posteromedial corner (medial tuberosity) of the bone. As noted by Remes (2008) the mediolateral expansion of the head exceeds the borders of the humeral shaft, although it lacks the pronounced incursion onto the proximo-posterior side of the shaft observed in *Riojasaurus* (and also to a lesser degree in *Massospondylus*, *Coloradisaurus* and *Adeopapposaurus*). Although present, the medial tuberosity is less pronounced than in the humeral head of most non-sauropodan sauropodomorphs (e.g. *Massospondylus*; *Lufengosaurus*; *Yunnanosaurus*) and is deflected slightly medially, as opposed to the posterolateral deflection of basal sauropodomorph taxa such as *Massospondylus*, *Coloradisaurus* and *Lufengosaurus* (= the Massospondylidae).

The medial surface of the proximal half is gently concave, whereas the lateral surface is almost entirely flat and is bordered anteriorly by the pronounced deltopectoral crest. This crest extends for roughly half of the length of the entire bone but is not as high and sharply demarcated as that of many non-sauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasurus; Lufengosaurus*). In the original description of *Antetonitrus* Yates and Kitching (2003:1754) had stated that “the deltopectoral crest does not extend for half the length of the humerus as it does in prosauropods”, however, the deltopectoral crest can be clearly shown to be at least half of the entire length of the humerus. In the smaller humerus, however, the deltopectoral crest is comfortably within the proximal half of the bone, possibly representing an effect of either ontogeny or variation.

In lateral view, the profile of the deltopectoral crest of *Antetonitrus* is rounded and anteriorly convex as in *Lessemsaurus* and *Leonerasaurus,* but with a steeper distal margin than in those taxa. In contrast, other non-eusauropod sauropodomorphs have a sharply delineated subrectangular profile with a straight and vertically orientated anterior margin (Pol et al. 2011). On the laterodistal margin of the deltopectoral crest there is a clear paramarginal sulcus, a possible autopomorphy that is shared with the smaller humerus (although a similar sulcus can be seen on the anterolateral surface of the deltopectoral crest

in *Riojasaurus* [PVL 3808] and *Melanorosaurus* [NM QR3314]). However, with the exception of this sulcus the deltopectoral crest is relatively uniform, lacking both sinuosity as well as the raised, irregular topography seen in a number of non-sauropodan sauropodomorphs (e.g. *Lufengosaurus*; *Riojasaurus*; *Massospondylus*).

The humeral shaft is short, robust and subcircular in cross-section, with a slight anterior curvature when viewed laterally. There is a relatively deep cuboid fossa (= intercondylar cavity) on the anterior surface of the distal humerus. This is a plesiomorphic feature generally absent in Eusauropoda that has been hypothesised as either accepting the radius during flexion (Bonnan and Senter 2007; Bonnan and Yates 2007) or as a receptacle for synovial fluids (Remes 2008: 251).

The posterior surface of the distal condyles is flat and extensive. Slight erosional damage makes it difficult to discern the true extent of the olecranon fossa; however, this appears to have been only weakly developed.

The distal condyles display a clear transverse expansion. However, damage to the lateral (radial) condyle makes it difficult to know the exact proportion and delimitation of each respective condyle, though extrapolating from the complete medial condyle gives a total mediolateral width of only 0.33 for the distal end. This is a similar ratio to that is observed in the more distally complete smaller humerus and is within the lower value-range for basal sauropodomorphs.

4.2.3 ULNA

There are three well preserved ulnae; a large left and right (BP/1/4952) of equal size probably belonging to the same individual; and a smaller right (BP/1/4952b) element. The distal end of the smaller ulna is slightly medially deflected compared to the larger elements. This may be due to differences in variation, ontogeny, or diagenesis. However, at this point it is impossible to distinguish between any of the above processes.

The complete larger right element (BPI/4952) is the best preserved and will form the focus of the following description (**Fig.11**). This ulna is 0.6 the length of the humerus (identical to

that of *Melanorosaurs:* NM QR 3314 and *Lessemsaurus*) and therefore possibly belonging to the same individual.

The ulna is a solid, robust bone that is most similar in general appearance to the ulnae of *Melanorosaurus* (SAM-PK-K3532: Bonnan and Yates 2007) and *Plateosauravus* (SAM 3351: Van Heerden 1979; Remes 2008). Proximally, the ulna of *Antetonitrus* possesses both the standard anterior process typical of saurischians and an additional lateral process characteristic of Sauropoda (Bonnan and Yates 2007:161). While not as distinctly tri-radiate as the Y-shaped proximal ulnae of the more derived eusauropods, the enlarged lateral process delimits a moderately deep radial fossa that is similar in appearance – albeit less developed – than the same process in *Vulcanodon*. This fossa may have been instrumental in facilitating the anteromedial rotation of the proximal radius around the ulna, a shift in forearm orientation now generally associated with the pronation of the manus (Bonnan 2003; Bonnan and Yates 2007). The possession of a distinct radial fossa distinguishes *Antetonitrus* from most basal sauropodomorph species which possess a more triangular proximal ulna with a blunt, rounded and short lateral process. A similarly developed lateral process is seen in *Melanorosaurus, Lessemsaurus* and the recently described *Aardonyx celesate* (Yates et al. 2010). As in *Melanorosaurus,* the anterior process of *Antetonitrus* is slightly concave proximally while the lateral process is strongly convex. A curious medially directed extension of the anterior process, especially marked in the larger right ulna, possibly represents an additional autopomorphy of *Antetonitrus*. Unfortunately, most of the anterior process appears to have been eroded prior to discovery in the companion left ulna, but a distinct medial deflection can still be seen. As in sauropodomorphs basal to the Vulcanodontidae (*Vulcanodon* + *Tazoudasaurus*) there is a strongly convex olecranon process that occupies the majority of the proximal surface.

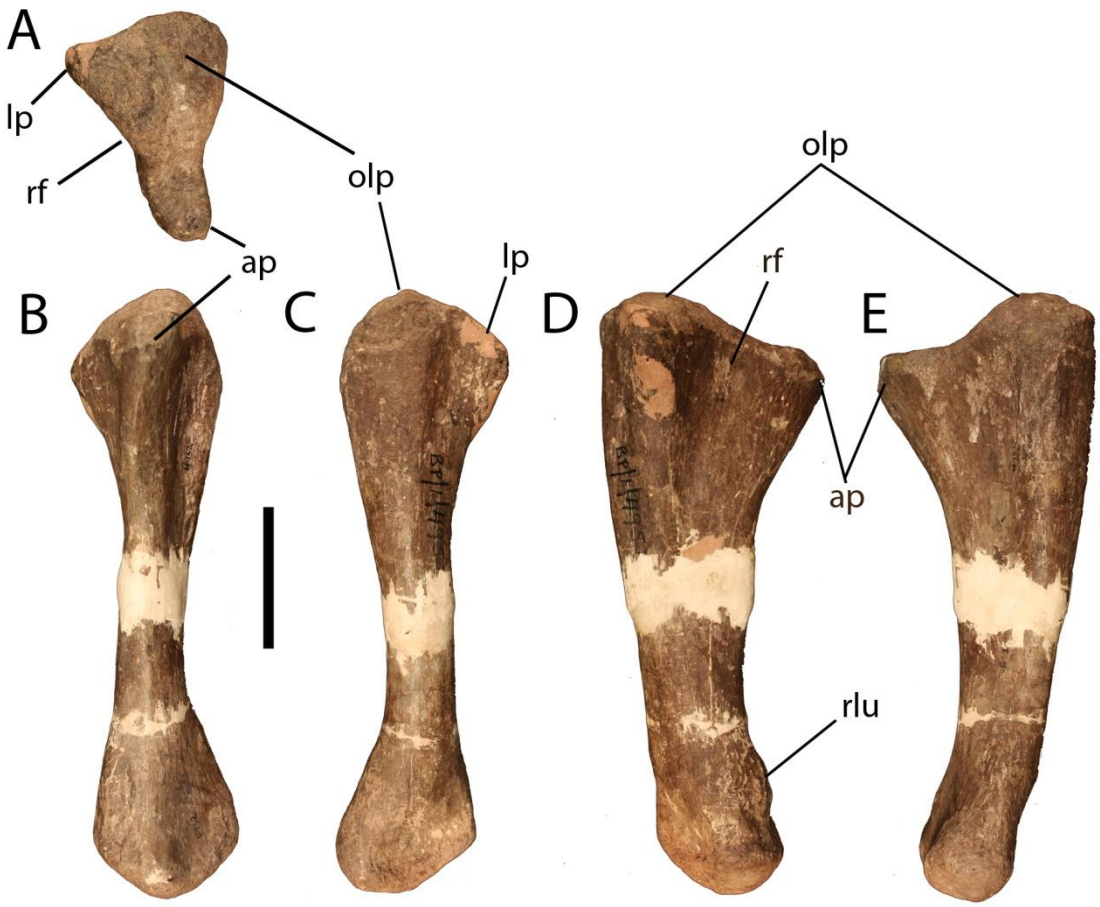

Fig. 11. *Antetonitrus ingenipes,* right ulna (BP/1/4952) in **A**, proximal; **B**, anterior; **C**, posterior; **D**, lateral; **E**, medial views. Abbreviations: ap, anterior process; lp, lateral process; olp, olecranon process; rf, radial fossa; rlu, radial ligament of the ulna. Scale bar = 10cm.

If the ulna is positioned so that the anterior and lateral processes transversely frame an anteriorly facing radial fossa, then the mediolateral expanse of the proximal surface is 0.38 of total ulna length, whereas the anteroposterior expanse of the distal bone is only 0.25 of total ulna length. However, as there still appears to be some confusion regarding the precise life orientation of the ulna in most large sauropodomorph taxa (Bonnan and Yates 2007 *contra* Pol and Powell 2007), the mediolateral expansion of the proximal end would only be 0.26 of total length if positioned so that the anterior process faces directly forward. In this case both proximal and distal ends display proportionately less mediolateral expansion than in *Lessemsaurus* (Pol and Powell 2007). Just distal to the radial fossa is a small, slightly rugose tubercle that most likely provided ligamentous attachments for the posterior edge of the proximal radius. On account of the autapomorphic deflection of the anteromedial

process the medial surface is equally as concave as the lateral surface, where the radial fossa is located. The posterior surface is gently convex and only about 0.66 of the proximal expansion of the other two surfaces.

The shaft is strongly elliptical and runs in the same plane as the anteromedial process before shifting to a transverse expansion in the distal third of the bone. The distal end is twisted about 15 degrees medially relative to the anteroposterior axis of the proximal surface. On the anterolateral corner of the distal end there is a pronounced tuberosity than corresponds with a similarly rugose bump on the posterior edge of the radius. These are the attachments for the radio-ulna ligament and can be seen in most basal sauropodomorph taxa (Cooper 1981). This condition appears to be the opposite of that in derived sauropods in which the distal radial fossa of the ulna cradles the radius distally (hypothesised as restricting movement at the wrist during quadrupedal locomotion [Bonnan 2003]). However, as a distinct bump is still present in the distal ulna of the vulcanodontid *Tazoudasaurus* (Allain and Aquesbi 2008: Fig. 22), this condition is therefore not seen as precluding the possibility of manual pronation. As mentioned by Remes (2008), the posterior side of the distal expansion is characterised by a large, pitted depression that merges with the transversely expanded distal articular surface. The distal surface is ovoid in shape, and bears the same rugose texture as the proximal end.

4.2.4 RADIUS

There is a single complete radius (BP/1/4952) that articulates well with the right ulna.

The radius is a straight, morphologically simple element with the proximal and distal expansion of both ends roughly equivalent and in the same plane (**Fig. 12**). This is in contrast to the morphology of basal sauropodomorph taxa such as *Massospondylus*, *Lufengosaurs* and *Seitaad* where the ends exhibit a modest axial twist with respect to one another. The proximal surface is subovoid with a simple planar articular surface that rises slightly posterolaterally. The long, elliptical proximal surface indicates the absence of a mobile rotary elbow joint, and hence 'active' manual pronation in *Antetonitrus* would have probably been rather limited. The shaft is elliptical in cross-section, being substantially wider anterposteriorly than mediolaterally. The lack of anteroposterior constriction of this bone

contrasts with the slender, rod-like shape of the radial shaft in a number of non-sauropodan sauropodomorphs (e.g., *Thecodontosaurus; Plateosaurus; Lufengosaurus; Riojasaurus*). In medial and lateral views the radius is markedly similar to that of *Melanorosaurs* (SAM-PK-K3532) and *Lessemsaurus* ('lateral' view in Pol and Powell, 2007: fig, 4c). The stout radius (and ulna) of *Melanorosaurus*, *Lessemsaurus* and *Antetonitrus* is also distinct from the markedly more elongate and slender radii of *Vulcanodon* and *Tazoudasaurus*. *Antetonitrus* also lacks the distinct medial bowing seen in more derived sauropods (e.g., *Vulcanodon*; *Camarasaurus*).

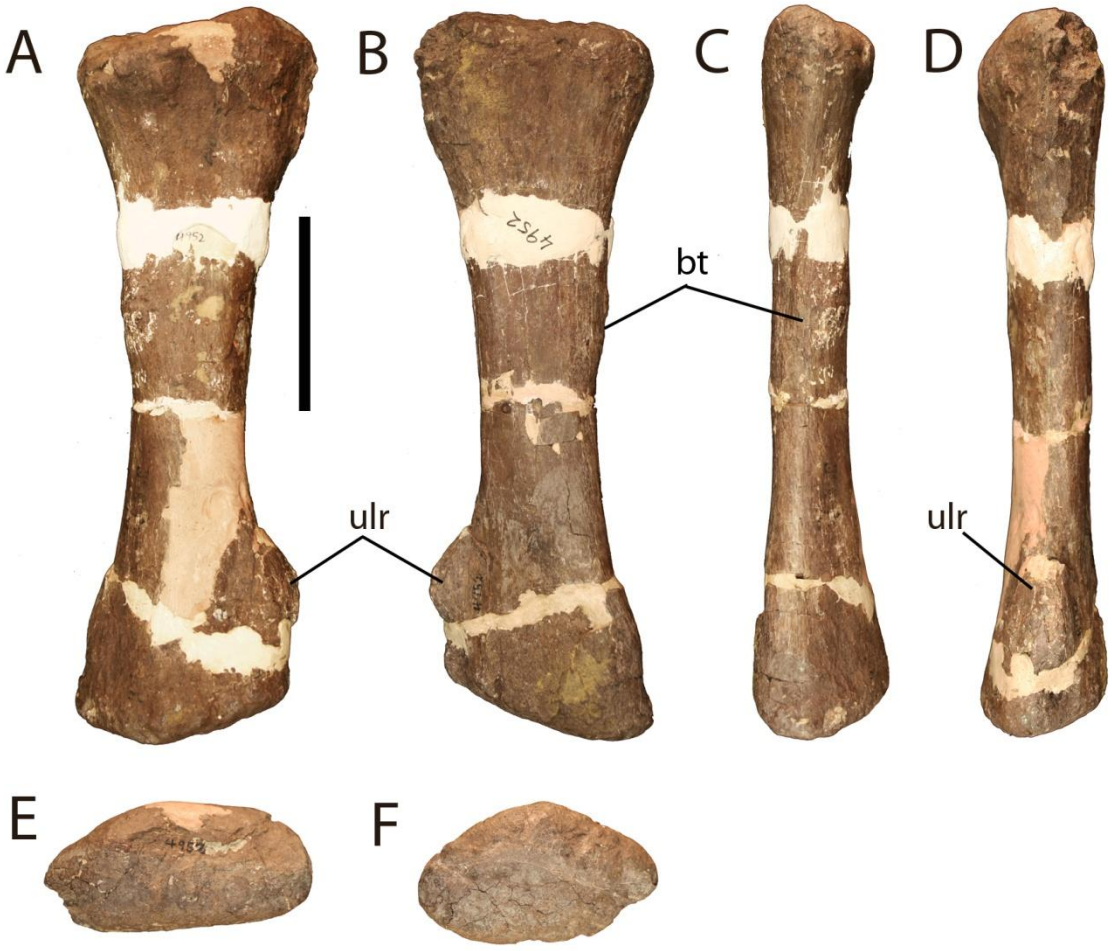

Fig.12. *Antetonitrus ingenipes*, right radius (BP/1/4952) in **A**, medial; **B**, lateral; **C**, anterior; **D**, posterior; **E**, proximal; **F**, distal views. Abbreviations: bt, biceps tubercle; ulr, ulnar ligament attachment of the radius. Scale bar = 10 cm.

Immediately proximal to the midshaft on the anterior edge there is a clear rugose tubercle for the attachment of the M. biceps (clearly present also in *Aardonyx*). The posterodistal edge displays a pronounced tuberosity that participates with a similar rugosity on the anteromedial corner of the ulna. This represents the attachment sites for ligamentous tissues that Bonnan (2003) and Bonnan and Yates (2007) have hypothesised as a supportive mechanism that limited the movement of the radius at the wrist. The distal articular surface is similar in size but slightly more ovoid than the proximal surface. It is gently convex and slopes upwards towards the posterior corner at a slightly greater angle than the similarly oriented proximal surface. A distal end that is proximally offset from the perpendicular angle formed with the long axis of the radial shaft has been hypothesised as further assisting in manual pronation by Remes (2008).

4.2.5 MANUS

The manus of *Antetonitrus ingenipes*, as preserved, is restricted to a right metacarpal I, its companion phalanx I.1, and two second metacarpals. In the original description of *Antetonitrus* (Yates and Kitching 2003) both second metacarpals were assigned to the holotype. However, although the second metacarpals are of equivalent size, both elements are from the same side, and therefore not belonging to a single individual. Previous reconstructions of the *Antetonitrus* hand (Yates and Kitching 2003; Remes 2008) have figured the second metacarpal as articulating with the lateral side of the first metacarpal, and therefore constituting the medial half of the metacarpus of a right hand. However, comparison with a fully articulated and fused inner carpus and metacarpus (BP/1/386) found amongst material referred to *Aardonyx* clearly indicates that both the second metacarpals of *Antetonitrus* belong to the left side, therefore showing that the figured articulation in Yates and Kitching (2003) and Remes (2008) could not be correct (see **Fig. 14**). Unfortunately, this reduces the scope of inference regarding the functional manoeuvrability and locomotory limitations of the *Antetonitrus* hand.

Metacarpal I: The first metacarpal in *Antetonitrus* is markedly stout and wide, with the mediolateral width of the flat proximal surface exceeding the proximodistal length of the bone (**Fig.13**). The mediolateral width of the proximal end is 1.18 the total length of the

bone. *Aardonyx* (1.12: BP/1/5379) and *Melanorosaurus* (NM QR3314) exhibit similarly short and broad first metacarpals, while *Lessemsaurus* is stouter still with a ratio of about 1.26. In contrast, all other derived non-sauropodan sauropodomorphs display proportionally longer first metacarpals with values ranging from the 0.65 - 0.7 seen in *Anchisaurus* and *Plateosaurus*, respectively, to the sub-equal ratios of *Yunnanosaurus*, *Lufengosaurus* and *Seitaad*. Eusauropodan taxa also display elongated first metacarpals, although the width/length ratio of *Shunosaurus* remains relatively stout at 0.94 (Zhang 1988: Fig. 49). The first metacarpal tends to lengthen closer to Neosauropoda, where the manus adopts the characteristic semi-tubular colonnade interpreted to be mechanically advantageous in supporting graviportal locomotion (Bonnan 2003). The proximal articular surface is constricted at the mid-point of the transverse plane, mainly on account of a proximomedial articular surface that is almost as expanded dorsoventrally as the proximolateral surface. Most other basal sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*) have a proximomedial articular surface that tapers to a clear point, hence the subtriangular proximal outline of their first metacarpals. In comparison, the proximal outline of the first metacarpal of *Antetonitrus* is keyhole in shape.

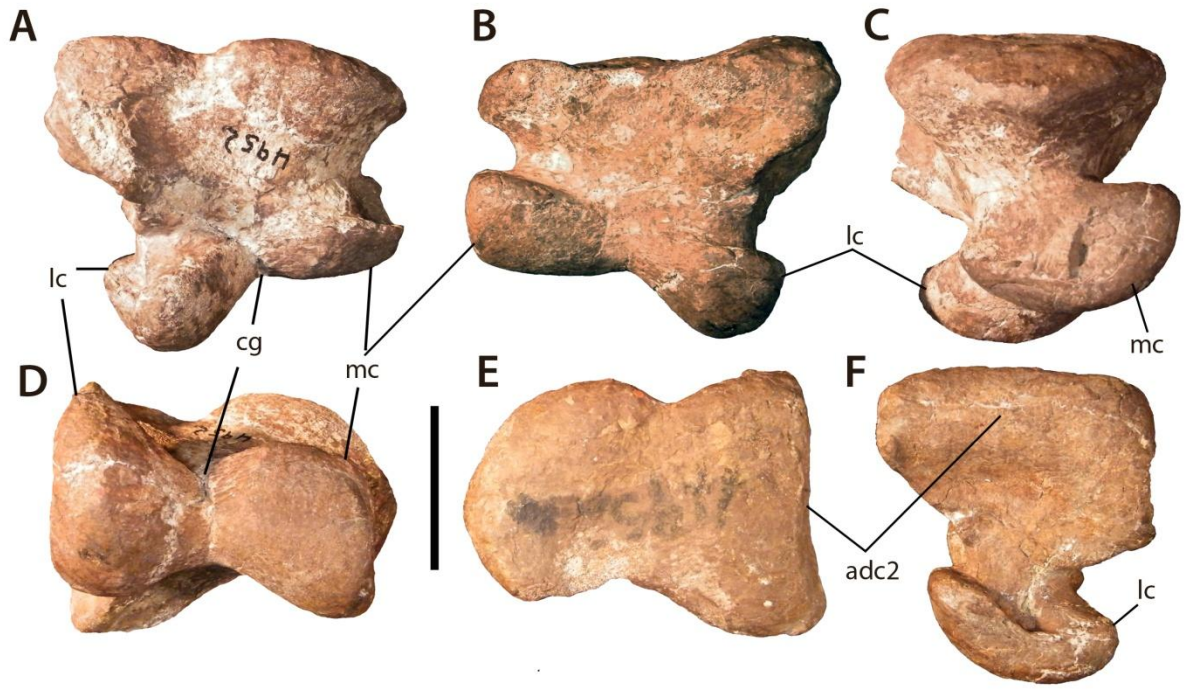

Fig. 13. *Antetonitrus ingenipes*, right metacarpal I (BP/1/4952) in **A**, dorsal; **B**, ventral; **C**, medial; **D**, distal; **E**, proximal; **F**, lateral views. Abbreviations: adc2, articular surface for distal carpal 2; cg, central ginglymus; lc, lateral condyle; mc, medial condyle. Scale bar = 5cm.

The lateral margin of the proximal surface of the first metacarpal exceeds the lateral extent of the lateral distal condyle. This feature is not commonly displayed in basal sauropodomorphs, although *Steitaad* and potentially *Lufengosaurus* show a similar proximolateral expansion (Young 1941; Sertich and Loewen 2010). The lateral margin of the proximal end is proximodistally broad and dorsoventrally extensive, possibly delimiting the synovial joint against which the second distal carpal would have rested –effectively precluding distal carpal I from articulating with the proximal surface of metacarpal II (Sereno 1999, 2007). The first metacarpal of *Lessemsaurus* also displays this proximolateral flattening, indicating that it may have been inset into the carpus in a similar fashion; a configuration clearly visible in the similarly proportioned manus of BP/1/386 (=*Aardonyx*). This configuration of carpus and metacarpus has been cited on numerous occasions (Sereno 1999; Galton and Upchurch 2004) as synapomorphic evidence uniting a monophyletic 'Prosauropoda'. However, although distal carpal II appears to have been lost by that point of sauropodomorph evolution, an intermediate morphology is potentially observable in the articulated manus of a juvenile individual of *Tazoudasurus* (Allain and Aquesbi 2008: Fig.23).

Distal to the synovial joint the proximolateral fossa (where the second metacarpal would have articulated) is large and dorsoventrally extensive, occupying the majority of the lateral surface. The medial surface, on account of the limited proximodistal extension of the shaft, is reduced to a short concave ridge between the proximal surface and the medial condyle. As in all non-eusauropodan sauropodomorphs, the distal articular condyles are strongly asymmetrical, with the medial condyle expanded mainly ventrally and the lateral condyle expanded mainly dorsally. The mediolateral width of the medial condyle exceeds that of the lateral condyle, a configuration also present (although to a slightly greater degree) in the first metacarpal of *Lessemsaurus* (PVL 4822). The opposite condition is observed in most non-sauropodan sauropodomorphs (e.g. *Plateosaurus*; *Massospondylus*; *Riojasaurus*; *Anchisaurus*). As in all non-eusauropodan sauropodomorphs the lateral condyle is much more distally expanded than the medial condyle, due mainly to the oblique orientation of the condyles. In *Lessemsaurus* this distal expansion of the lateral condyle appears to have been somewhat reduced compared to the condition observed in *Antetonitrus*. The articular surfaces of the distal condyles presents a ginglymoidal joint of approximately 180 degrees that is directed slightly more ventrally than dorsally, observable also in *Lessemsaurus*,

Aardonyx and most basal sauropodomorphs. The collateral ligament pit on the lateral condyle is slightly more excavated than on the medial.

Metacarpal II: The second metacarpal in *Antetonitrus* is 1.43 the length of metacarpal I. This is within the general range of most non-sauropodan sauropodomorphs (e.g. *Thecodontosaurus*; *Anchisaurus*; *Riojasaurus*; *Plateosaurus*; *Massospondylus*) while being proportionally longer than that of *Jingshanosaurus* (1.15) and the newly described basal sauropodomorph *Steitaad ruessi* from the early Jurassic of Utah which appears to have had subequally sized first and second metacarpals (Sertich and Loewen 2010). Interestingly, the second metacarpal of *Lessemsaurus* is conspicuously elongated at 1.78 the length of the first metacarpal, but it is highly probable that both elements belong to different individuals (although a similar relationship cannot be discounted in *Antetonitrus*).

The proximal articular surface of the second metacarpal in *Antetonitrus* is strongly convex and rhomboidal in general outline. There is a distinct dorsolateral flange that begins proximally and extends for half the length of the bone that may have abutted with the third metacarpal proximomedially. This acute lateral flange of bone is common in a number of non-eusauropodan sauropodomorph taxa, including *Lessemsaurus*, *Plateosaurus*, *Massospondylus* and BP/1/386 (*contra* Pol and Powell 2007), while being absent in other non-eusauropodan taxa (e.g., *Yunnanosaurus*; *Tazoudasaurus*). The dorsomedial corner of the proximal surface also displays an incipient swelling, although this is considerably less developed than on the dorsolateral corner. Together the dorsolateral flange and dorsomedial swelling delimit a distinctly concave proximodorsal surface. The medioventral corner of the proximal surface houses a small tubercle that probably cradled the first metacarpal ventrally. Just proximal to midpoint on the ventrolateral margin of the shaft there is a distinct bifurcated tuberosity that is similar to that seen on the ventrolateral margin of the shaft in BP/1/386. This process is present in both of the *Antetonitrus* second metacarpals and potentially represents an apomorphy of both *Antetonitrus* and *Aardonyx* as a similar process is observed nowhere else within the sauropodomorph record. The functional significance of this process is difficult to speculate upon, although it may indicate that the manus in *Antetonitrus* (and potentially *Aardonyx*) was relatively tightly bound, potentially representing an additional supporting mechanism during regular or sporadic quadrupedal motion.

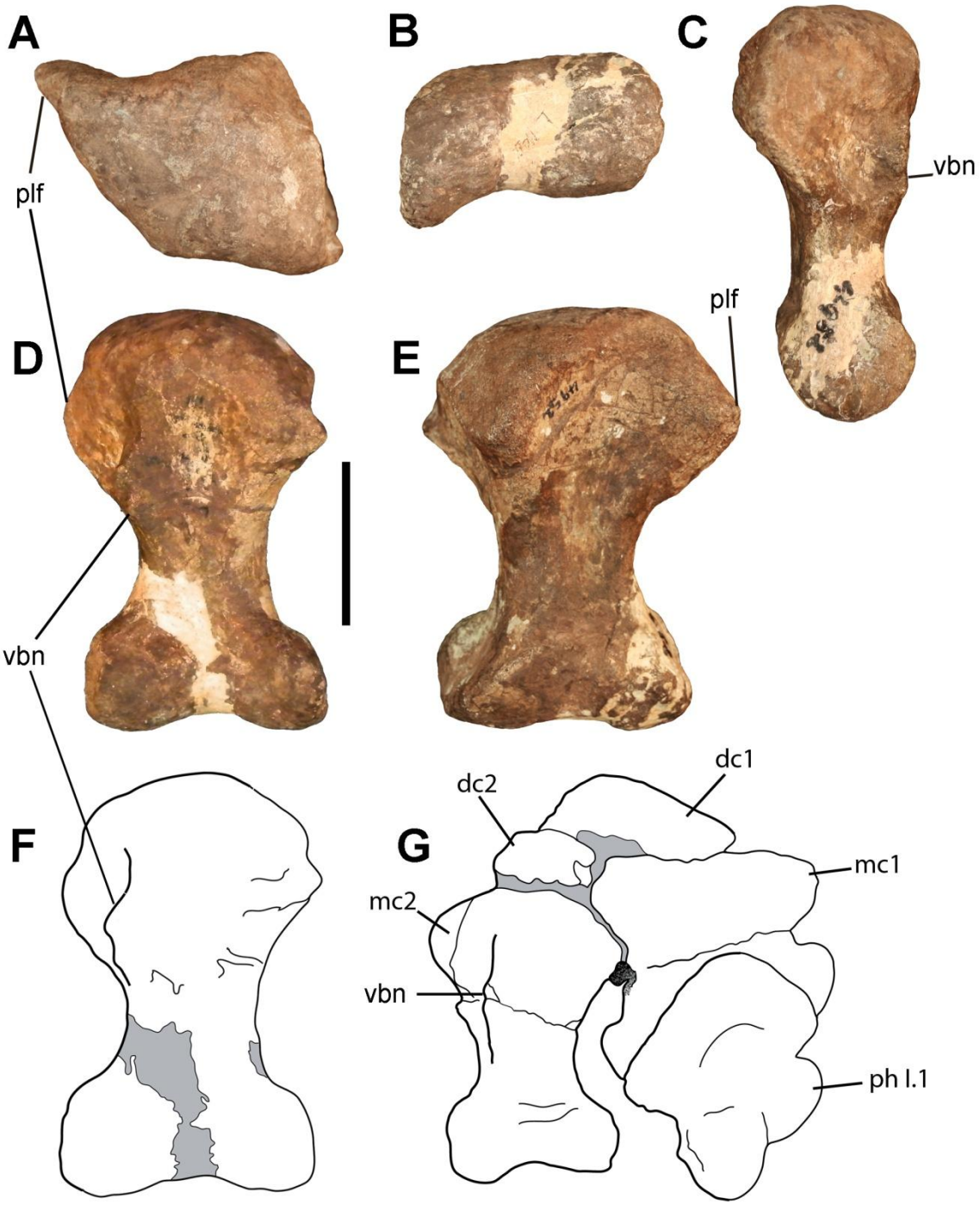

Fig. 14. *Antetonitrus ingenipes*, left metacarpal II (BP/1/4952) in **A**, Proximal; **B**, distal; **C**, lateral; **D**, ventral; and **E**, dorsal views. **F**–**G**: line drawings of **F**, *Antetonitrus ingenipes* second metacarpal in ventral view and **G**, referred *Aardonyx celestae* (BP/1/386) left carpus and metacarpus in ventral view. Abbreviations: dc1, distal carpal 1; dc2, distal carpal 2; mc1, metacarpal I; mc2, metacarpal II; ph I.1, manual phalanx I.1; plf, proximolateral flange; vbn, ventral bifurcated notch. Scale bar = 5cm

The shaft is notably short and stout, with its minimum transverse width 0.35 times the total proximodistal length of the bone. This contrasts with a ratio of 0.2 to 0.25 in most derived

sauropodomorphs (e.g., *Plateosaurus*; *Riojasaurus*; *Yunnanosaurus*; *Tazoudasaurus*), although the eusauropodan taxon *Shunosaurus lii* displays the exact same ratio as *Antetonitrus* (Zhang 1988). The distal articular condyles are symmetrically developed and minimally differentiated from one-another, although the ventral corner of the medial condyle is slightly more acute and ventrally expanded than in the lateral condyle. There is no evidence of a collateral ligament fossa on either condyle.

Manual phalanx I.1: The manual phalanx I.1 of *Antetonitrus* is a short and robust element with a proximal articular surface that is mediolaterally wider than the total proximodistal length of the bone (**Fig.15**). These same proportions are seen in *Lessemsaurus* (although this is only true when measured from the dorsal surface), whereas most other non-sauropodan sauropodomorphs tend to have a manual phalanx I.1 that is slightly longer than wide (e.g *Plateosaurus*; *Riojasaurus*; *Seitaad*). Although the proximal medial articular facet is missing, it is clear that it would have been much reduced compared to the extensively subcircular lateral articular facet, as in all sauropodomorphs. The proximoventral heel of manual phalanx I.1 is deeper proximally than the proximodorsal lip, as is common to all non-eusauropodan sauropodomorphs. The shaft, being extremely short, is represented by no more than a subtle mediolateral constriction between the proximal and distal articular surfaces. However, the damage sustained by the proximomedial corner of the bone makes it difficult to confirm the precise degree of transverse constriction in the shaft. As is typical of all non-eusauropodan sauropodomorphs, the distal condyles are twisted laterally along the proximodistal axis in relation to the proximal surface. In *Antetonitrus* this degree of axial torsion is approximately 30 degrees, similar to the low degree or torsion seen in *Lessemsaurus* and a number of basal sauropodomorphs (e.g. *Thecodontosaurus*; *Plateosaurus*; *Riojasaurus*), but contrasting with species such as *Massospodylus*, *Lufengosaurus* and *Yunnanosaurus* that exhibit a highly twisted phlananx I.1 of about 45 degrees. The distally twisted phalanx I.1 of non-sauropodan sauropodomorphs, coupled with the asymmetrically developed lateral condyle of metacarpal I, would have exerted a strong medial cant to the ungual phalanx of manual digit I during flexion (Cooper 1981; Galton and Upchurch 2004). The ability of sauropodomorph dinosaurs to hyperextend the first digit dorsally is well known (Galton and Upchurch 2004), and was facilitated by a distal ginglymus of the first manual phalanx that extended along the dorsoventral curvature of the

bone at an angle of 180 degrees. This morphology is well recorded in phalanx I.1 of *Antetonitrus*, where the distal articular surface extends well above the dorsal surface of the shaft. It is possible that hyperextension of the first manual digit represents an adaptive response to the need to raise the thumb above the substrate while walking or standing quadrupedally/tripedally (Galton and Upchurch 2004), although it is possible that it merely represents an augmentation of the dexterity required for efficient grasping and feeding (Remes 2008; Mallison 2010b).

The distal articular condyles extend further ventrally than dorsally, and are also mediolaterally wider and more divergent ventrally than dorsally, as is common to most non-sauropodan sauropodomorphs. The collateral ligament pit appears to have been much more deeply developed on the medial condyle than on the lateral. This same relationship is described for *Lessemsaurus* (Pol and Powell 2007).

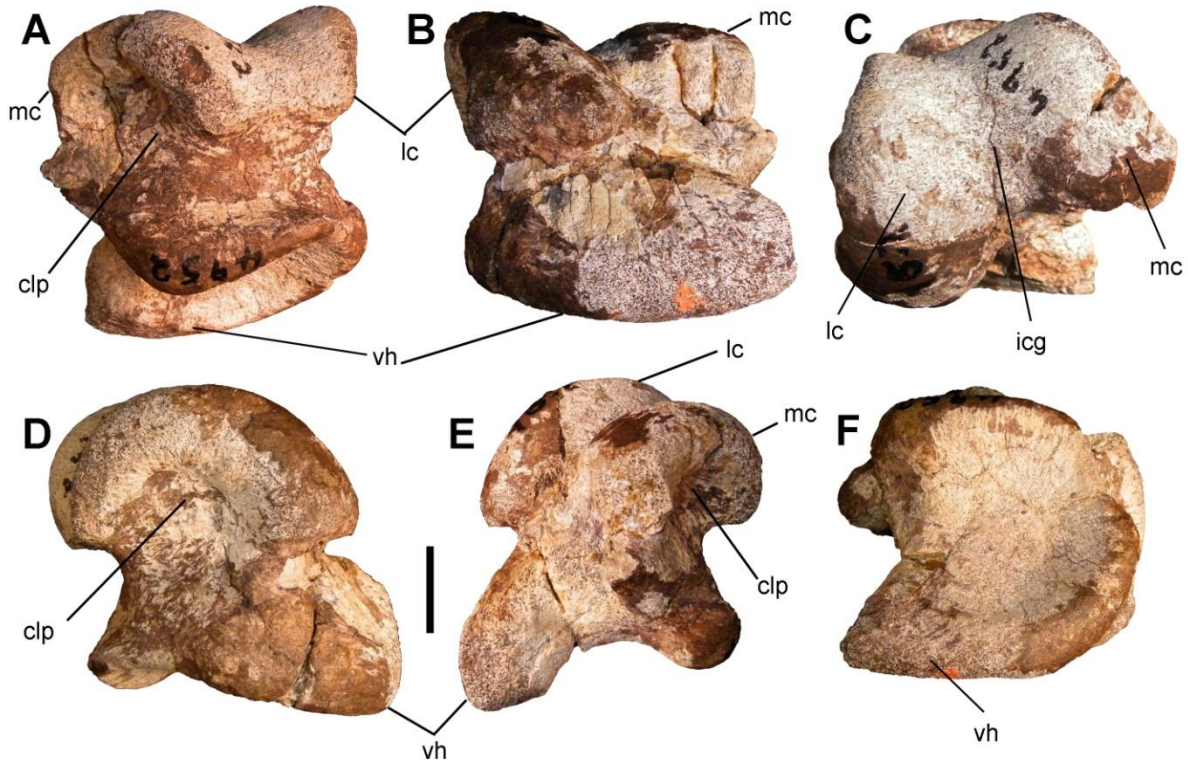

Fig.15. *Antetonitrus ingenipes,* right manual phalanx I.1 (BP/1/4952) in **A**, dorsal; **B**, ventral; **C**, distal; **D**, lateral; **E**, medial; **F**, proximal views. Abbreviations: clp, collateral ligament pit; icg, intercondylar groove; lc, lateral condyle; mc, medial condyle; vh, ventral heel. Scale bar = 2cm.

4.2.6 ILIUM

Amongst the referred material of *Antetonitrus* (NM QR1545) housed in the collections of the National Museum there are two large Ilia, a left and a right. Given the close morphological similarity of the appendicular elements to the BPI material (see above: Referred Material in 'Results' section) it is assumed that the ilium described herein also belongs to *Antetonitrus* (or a taxon of extremely close taxanomic affinity). Both elements are tentatively referred to different individuals as the left is both slightly smaller and of dissimilar preservation to the right. The right, although missing the pubic peduncle, is also considerably better preserved, and will form the main focus of the following description.

Fig. 16. *Antetonitrus ingenipes*, right ilium (NM QR 1545) in lateral view. Mesh pattern indicates areas that have been replaced with plaster. Maximum length (anteroposteriorly) = 565mm

The ilium of *Antetonitrus* retains the plesiomorphic condition seen in most non-eusauropodan sauropodomorphs: the iliac blade is anteroposteriorly elongate and dorsoventrally low*;* the preacetabular process is short, pointed and does not appear to have exceeded the anterior extent of the pubic peduncle (although as the latter is broken, this cannot be said with certainty). This morphology is present in most basal sauropodomorph taxa (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*), although some species are exceptional in having preacetabular processes that extend beyond the anterior margin of the pubic peduncle (*Anchisaurus*; *Leonerasaurus*). This latter condition is also typical of

Tazoudasaurus + Eusauropoda, although in that group the preacetabular process is greatly expanded dorsoventrally and the apex is proportionally blunter compared to non-eusauropodan sauropodomorphs. The preacetabular process of *Antetonitrus* appears to have exhibited/retained a slight ventral deflection, in contrast to the anteriorly directed preacetabular process seen in *Lessemsaurus*, although this deflection is very subtle.

The mediolaterally thin anterodorsal margin of the iliac blade is missing in the better preserved ilium, making it difficult to distinguish if a similar 'step' between the preacetabular process and the dorsal margin of the iliac blade (as seen in *Riojasurus* and some specimens of *Massospondylus*) was present. The left ilium of NM QR1545 does preserve this area, however, whereupon the preacetabular process appears to have presented a continuum with the shallowly convex dorsal margin of the blade. Compared to most basal sauropodomorphs (e.g. *Massospondylus*; *Melanorosaurus*) and more derived taxa (i.e. eusauropods) the acetabular region is anteroposteriorly, dorsoventrally and mediolaterally massive. The supracetabular crest appears to have been well developed on the lateral surface of the pubic peduncle and rises as a pronounced lateral flange along the anterodorsal margin of the acetabulum. Derived sauropodan taxa (e.g. *Tazoudasaurus*; *Shunosaurus*) lack such extensive development of the supracetabular crest, although it is worth noting that the sharp, laterally flared morphology of this process in *Antetonitrus* appears to have been historically augmented with plaster. This augmentation makes it difficult to determine if the laterally 'overhung' rim of the supracetabular crest (i.e. in lateral view the lateral margin of the supracetabular crest is deflected ventrally so as to obscure the dorsal apex of the acetabulum from view) is a true autopomorphy of *Antetonitrus*, or if this is simply an artefact of the reconstruction of the supracetabular crest in NM QR1545.

Anteriorly, the acetabulum is markedly concave and mediolaterally extensive, being almost hemispherical at its anterodorsal margin. As the pubic peduncle is missing it is difficult to ascertain whether the same anteromedial wall of the acetabulum observed in *Lessemsaurus* (Pol and Powell 2007) was present in *Antetonitrus*. However, an isolated and unreferred ilium (BP/1/5003) collected from the same region of the Lower Elliot Formation as the type assemblage of *Antetonitrus* does display an extensive flange of bone on the posteromedial wall of the pubic peduncle. This ilium is a close match to NM QR1545 in both proportions

and salient characteristics (including a ventrolaterally overhung supracetabular crest), and is tentatively referred to *Antetonitrus* here.

The ischial peduncle also appears to have been 'repaired' with plaster, but it is nonetheless evident that the ischial peduncle was ventrally extensive as in most non-eusauropodan sauropodomorphs. In contrast, Sauropoda + Eusauropoda have highly reduced or entirely absent ischial peduncles. It is also possible that the ischial peduncle of *Antetonitrus* exhibited an incipient heel on its posteroventral corner, although this was probably less developed than in a number of other sauropodomorph taxa (i.e. *Plateosauravus; Plateosaurus*; *Riojasaurus*;).

On the ventral surface of the posterior blade a thin brevis crest extends from the posterodorsal margin of the ischial peduncle to the ventral surface of the postacetabular process. As in most derived sauropodomorphs the posterior iliac blade is relatively flat and featureless, and the absence of a brevis shelf results in the concomitant absence of a brevis fossa. The postacetabular process is not entirely preserved but appears to have been bluntly rounded to sub-rectangular in shape with a distinct posteroventral corner, as in a number of other non-eusauropodan sauropodomorphs (e.g. *Riojasaurus*; *Yunnanosaurus*; *Massospondylus* BP/1/4693). In contrast, taxa such as *Plateosauravus* and *Plateosaurus* display much sharper, square-ended postacetabular process. Consistent with the basal sauropodomorph condition the postacetabular process is anteroposteriorly extensive, lacking the extreme reduction of the postacetabular region seen in Sauropoda + Eusauropoda. On the anterodorsal surface of the postacetabular process there is a pronounced striated swelling. This represents the thickest point of the dorsal margin of the ilium in NM QR1545 and is possibly related to the attachment for the M. iliotibialis (Langer 2003).

4.2.7 PUBIS

A single large left pubis is preserved (**Fig. 17**).

The pubis is similar in overall proportions to most non-eusauropodan sauropodomorphs being relatively long and slender. The maximum mediolateral width of the pubis (measured where the obturator plate meets the pubic apron) is approximately 0.37 of total proximodistal length. This is slightly more squat but in the same basic range as other non-eusauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*; *Aardonyx*; *Lessemsaurus*; *Tazoudasurus*), being closest to the condition observed in *Vulcanodon* (Cooper 1984). In contrast, *Spinophorosaurs* + Eusauropoda display proportionally shorter and wider pubes (Remes et al. 2009). The obtorator plate (= proximal plate *sensu* Pol and Powell 2007) is reduced in much the same manner as most non-sauropodan sauropodomorphs, representing only approximately 0.30 of total proximodistal length. This contrasts with the condition present in *Vulcanodon*, *Tazoudasaurus*, *Spinophorosaurus* and basal eusauropods in which the proximal plate generally occupies at least 0.40 – 0.50 of total pubic length. Interestingly, the pubis of *Lessemsaurus* is described as presenting the latter condition (Pol and Powell 2007: Text-Fig. 7), however, close examination of PVL 4822/61 yields a more conservative ratio of approximately 0.37 for that taxon.

The iliac peduncle is flat proximally and markedly thick anteroposteriorly, being proportionately thicker than the same process in a number of basal sauropodomorph taxa (e.g. *Massospondylus*; *Aardonyx*; *Yunnanosaurus*). The acetabular portion of the pubis is equally broad but very short, lying posteromedial to the iliac peduncle and proximal to the anteriorly directed puboischial symphysis. The latter is broad proximally but tapers distally, becoming thin and sinuous for the majority of its length.

The obturator foramen is obscured by both plaster and matrix, but its dimensions appear to have been reduced as in derived sauropodomorphs and certainly would not have exceeded those of *Vulcanodon*. Distal to the obturator plate the pubic apron is flat, proximodistally straight, latermedially wide and oriented transversely. This condition is plesiomorphic amongst basal saurischians including all non-eusauropodan sauropodomorphs (e.g. *Vulcanodon*; *Tazoudasurus*); although the recently described *Spinophorosaurus,* which is

hypothesised to be the sister-taxon to Eusauropoda (Remes et al. 2009), appears to represent an exception. The anterior margin of the pubic apron is roughly confluent with anterior margin of the iliac pedicle in mediolateral view. This appears to have been the primitive condition for Dinosauria but was independently gained several times in Sauropodomorpha (e.g. *Antetonitrus*; *Saturnalia*; *Efraasia*; *Cetiosaurus*), whereas most sauropodomorphs/sauropods (e.g. *Massospondylus*; *Coloradisaurus*; *Lessemsaurus; Patagosaurus; Omeisaurus*) present proximal plates that are anteriorly expanded beyond the anterior margin of the pubic apron.

The lateral margin of the apron is thick, rounded and with a similar degree of lateral concavity (when viewed in anterior aspect) as that evinced by *Lufengosaurus*, *Lessemsaurus* and *Tazoudasurus* (and possibly *Vulcanodon*). In contrast, the medial edge is much thinner, straighter and irregularly preserved along what would have been the symphyseal connecting suture with the right pubic blade. Along its length the transverse width of the pubic apron is approximately 0.44 of its proximodistal length. This is a slightly higher ratio than a number of basal sauropodomorphs (e.g. *Massospondylus*; *Plateosaurus*; *Aardonyx*) which generally display a ratio of around 0.27 -0.38, approaching instead the ~ 0.50 observed in *Vulcanodon* and *Tazoudasurus*. It is possible that the general pubic proportions of *Antetonitrus* were very similar to that of *Lessemsaurus*, but the medial edge of the pubic apron in PVL 4822/61 has sustained significant damage, rendering estimates of the transverse dimensions of the pubic apron in *Lessemsaurus* problematic.

As in *Lessemsaurus*, the distal end of the pubis is slightly expanded anteroposteriorly, but less so than in other non-eusauropodan sauropodomorphs such as *Massospondylus*, *Plateosaurus*, *Vulcanodon* and *Tazoudasurus*.

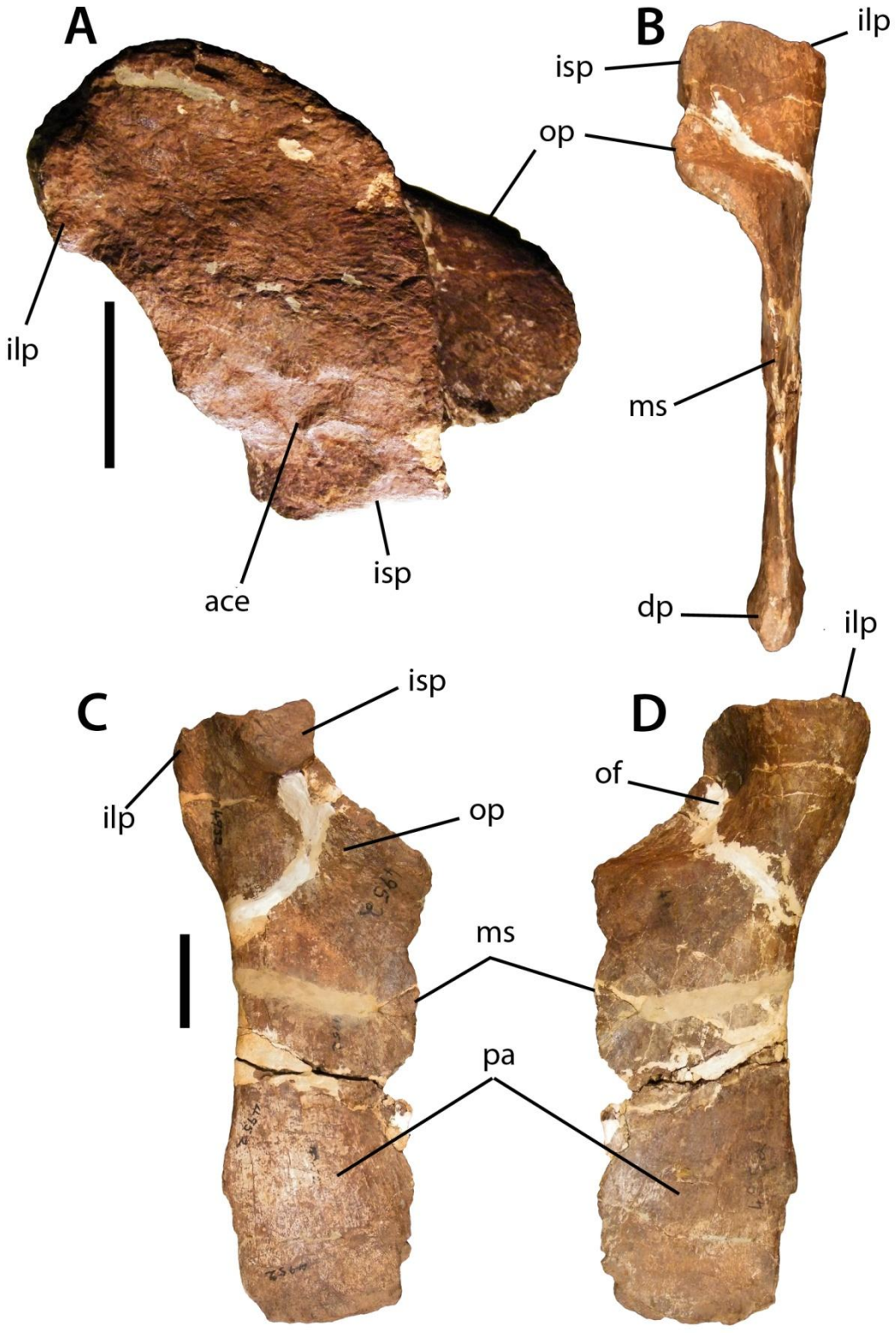

Fig.17. *Antetonitrus ingenipes*, left pubis (BP/1/4952) in **A**, proximal (anterior is up); **B**, medial; **C**, posterior; and **D**, anterior views. Abbreviations: ace, acetabulum; dp, distal expansion; ilp, iliac peduncle; isp, ischial peduncle; ms, medial symphisis; of, obturator foramen; op, obturator plate; pa, pubic apron. Scale bar = 10cm

4.2.8 FEMUR

There is a single large left femur (**Fig. 18**) (BPI/1/4952). Although well-preserved, it appears to have undergone a modest degree of postmortem distortion, so that the distal condyles are slightly flattened anteroposteriorly and deflected anterolaterally with respect to the anterior surface of the femoral shaft. The resulting effect is subtle, however, and while there is the possibility that this distortion might be exaggerating the placement of certain femoral processes (such as the acute medial position of the fourth trochanter), the uniform and undamaged contours of the bone suggest that its essential morphology remains intact.

The femur is a stout, robust element, that, while large (780mm), is not significantly more so than the larger humerus, with the resulting humeral/femoral ratio slightly higher than 0.90. The implications of this relatively elevated humerus/femur ratio are treated at length in the discussion.

The head of the femur is directed perpendicular to the proximodistal axis of the shaft and in dorsal view is deflected slightly anterior to the mediolateral plane, though significantly less so than the approximately 45 degrees seen in basal sauropodomorph taxa such as *Plateosaurus*. The posterolateral corner of the femoral head is slightly damaged, such that most of the greater trochanter is missing, however, its distal segment can be seen terminating adjacent to the lesser trochanter and was possibly separated from the latter via a shallow trochanteric ridge. In lateral view the sigmoid curvature of the femoral shaft is highly reduced compared to most non-sauropod sauropodomorphs, being similar in appearance to that of *Melanorosaurus* (NM QR1551), *Riojasaurus* and *Camelotia* (Galton 1998). However, it is possible that the anteroposterior flattening of the distal condyles means that the lateral curvature of the distal half is less than it would have been in life. The femur is straight in anterior or posterior view, as is typical of most saurischians and all derived sauropodomorphs (Rauhut et al. 2011). The femoral shaft is strongly elliptical throughout its length, with the anteroposterior width approximately 0.66 of the transverse width. This marks a departure from the subcircular femoral shafts of most non-sauropodan sauropodomorphs and places the basic femoral morphology of *Antetonitrus* intermediate between that of *Melanorosaurus* and *Isanosaurus* + Sauropoda.

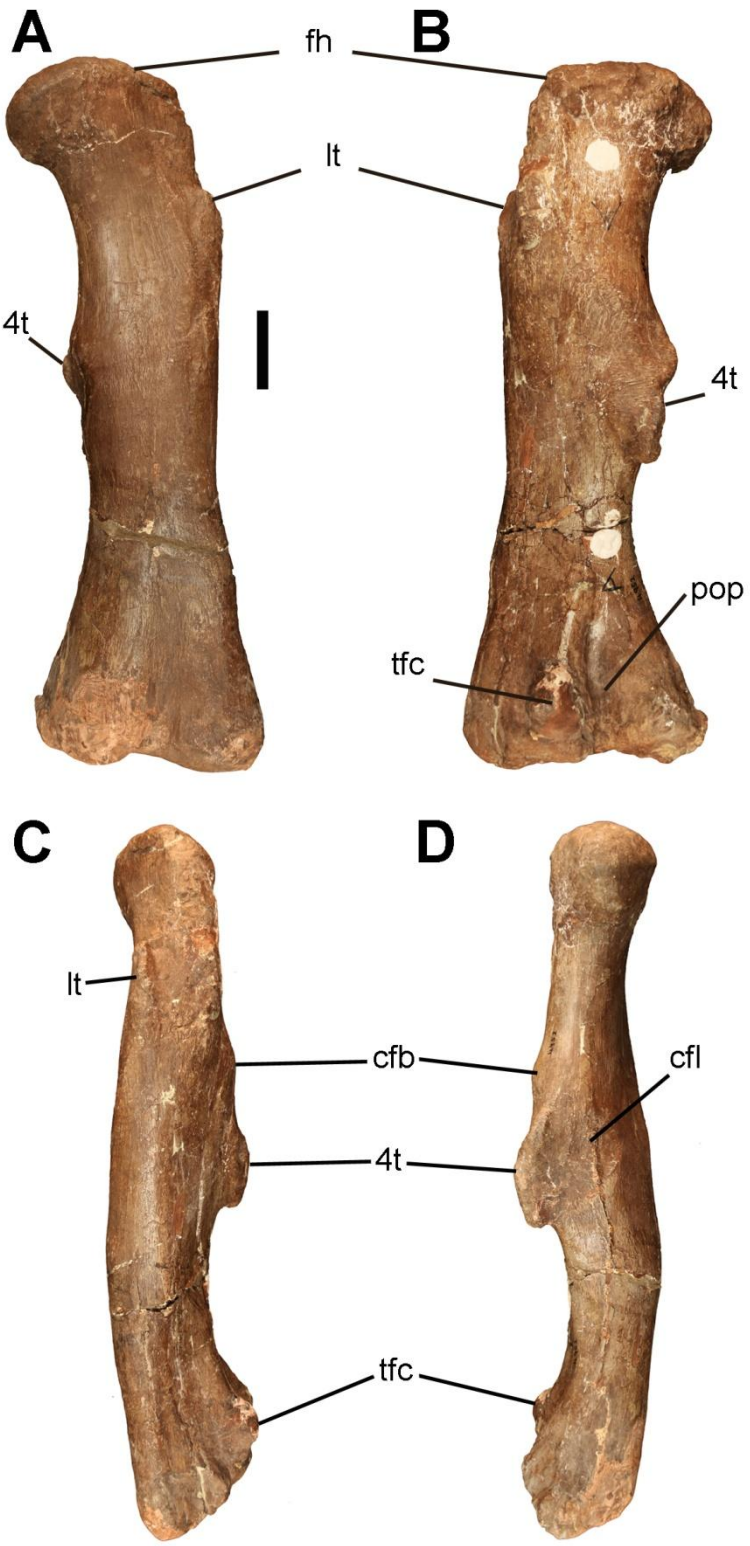

Fig. 18. Antetonitrus ingenipes, left femur (BP/1/4952) in **A**, anterior; **B**, posterior; **C**, lateral; and **D**, medial views. Abbreviations: 4t, fourth trochanter; cfb, M. caudofemoralis brevis insertion site; cfl, M. caudofemoralis longus insertion site; fh, femoral head; lt, lesser trochanter; pop, popliteal fossa; tfc, tibiofibular crest. Scale bar = 10cm.

The lesser trochanter is a well-developed ridge that is similar in relative size to most basal saurpodomorphs (e.g. *Melanorosaurus*; *Riojasuarus*; *Eucnemesaurus*). It rises steeply with its proximal termination distal to the distal margin of the femoral head. The sheet-like distal end merges gradually with the femoral shaft, terminating roughly parallel to the proximal margin of the fourth trochanter. The lesser trochanter in *Antetonitrus* is axially straight, lacking the subtle oblique orientation observed in a number of non-sauropodan taxa (e.g. *Plateosaurus*; specimens of *Massospondylus*; material referred to *Aardonyx* [BP/1/386]). Of special note is the prominent lateral placement of the lesser trochanter, being partially visible in posterior view. Although the lateral migration of this process presages the condition in Sauropoda, in that group the lesser trochanter is reduced to a negligible bump on the lateroproximal corner of the shaft (Carrano 2005).

The fourth trochanter is an especially well-developed crest located at femoral mid-length. By all indications this process and the adjacent bone surface is hypertrophied to an autopomorphic extent within Sauropodomorpha. In most basal sauropodomorph taxa (e.g. *Saturnalia*; *Plateosaurus; Jingshanosaurus*) the fourth trochanter projects as a pronounced flange from the posterior surface of the femoral shaft. While the degree of trochanteric projection in these taxa is similar to that of *Antetonitrus*, the area of bone immediately surrounding the fourth trochanter is relatively smooth and flat (with the exception of the medial fossa where the M. caudofemoralis longus inserts). In contrast, the fourth trochanter in *Antetonitrus* is bordered posteriorly by an elevated surface scored with extensive striations. This begins proximal to the fourth trochanter in the middle of the posterior femoral shaft, where it descends mediodistally to meet the top of the fourth trochanter on the medial surface of the shaft. This surface is hypothesised as the insertion area for the M. caudofemoralis brevis, which has been reconstructed in a similar position in a number of dinosaurian taxa (Dilkes 2000; Carrano and Hutchinson 2002; Dilkes et al. 2012).

The apical surface of the fourth trochanter is crescent shaped with the proximal half deflected anteriorly and the distal half in line with the proximodistal orientation of the shaft. This orientation of the fourth trochanter, along with its steep distal termination, is similar to that seen in *Lessemsaurus* (Pol and Powell 2007) (although a curved fourth trochanter with steep ('semi-pendent') distal margin has also been described for specimens of *Eucnemesaurs* [Yates 2007a]). The fourth trochanter of *Antetonitrus* is sub-rectangular in

profile, similar to most non-sauropodan sauropodomorphs, but different to the more rounded profile described for *Eucnemesaurus* and *Riojasaurus* (Bonaparte 1972; Yates 2007a). The medial surface of the fourth trochanter bears a shallow depression and is markedly rugose, housing as it would have the insertion of the M. caudofemoralis longus (Langer 2003). The medial placement of the fourth trochanter at mid-shaft distinguishes *Antetonitrus* from most basal sauropodomorphs which tend to have a more posteriorly positioned fourth trochanter located in the proximal half of the bone. Instead, the placement is similar to that of *Melanorosaurs* + Sauropoda (*sensu* Yates 2007a, b). However, all derived sauropods beginning with *Isanosaurus* and *Vulcanodon* have reduced muscle attachment sites on the femur. The opposite condition is seen in *Antetonitrus*, where the rugose raised and pitted areas surrounding the fourth trochanter account for approximately 0.43 of the total circumference of the femoral shaft (measured just proximal to fourth trochanter). The functional significance of these muscular proxies will be addressed in the Discussion.

Despite the distortion of the distal end of the femur it is still possible to observe the mediolateral expansion of the distal condyles and the deep, proximodistally extensive popliteal fossa on the posterior surface. The tibiofibular crest appears (it has been partially repaired with plaster) to have been reduced compared the posteriorly-projecting flange of bone seen in most basal sauropodomorphs (e.g., *Plateosauravus*, *Plateosaurus*, *Massospondylus*, and *Aardonyx*) and is wider mediolaterally than it is proximodistally high, as in *Glacialisaurus, Melanorosaurus* and possibly *Jingshianosaurus*. It is possible that this represents a secondary reduction in the development of the tibiofibular crest that *Antetonitrus* shares with more derived sauropodan taxa (e.g. *Tazoudasaurus*; *Shunosaurus*).

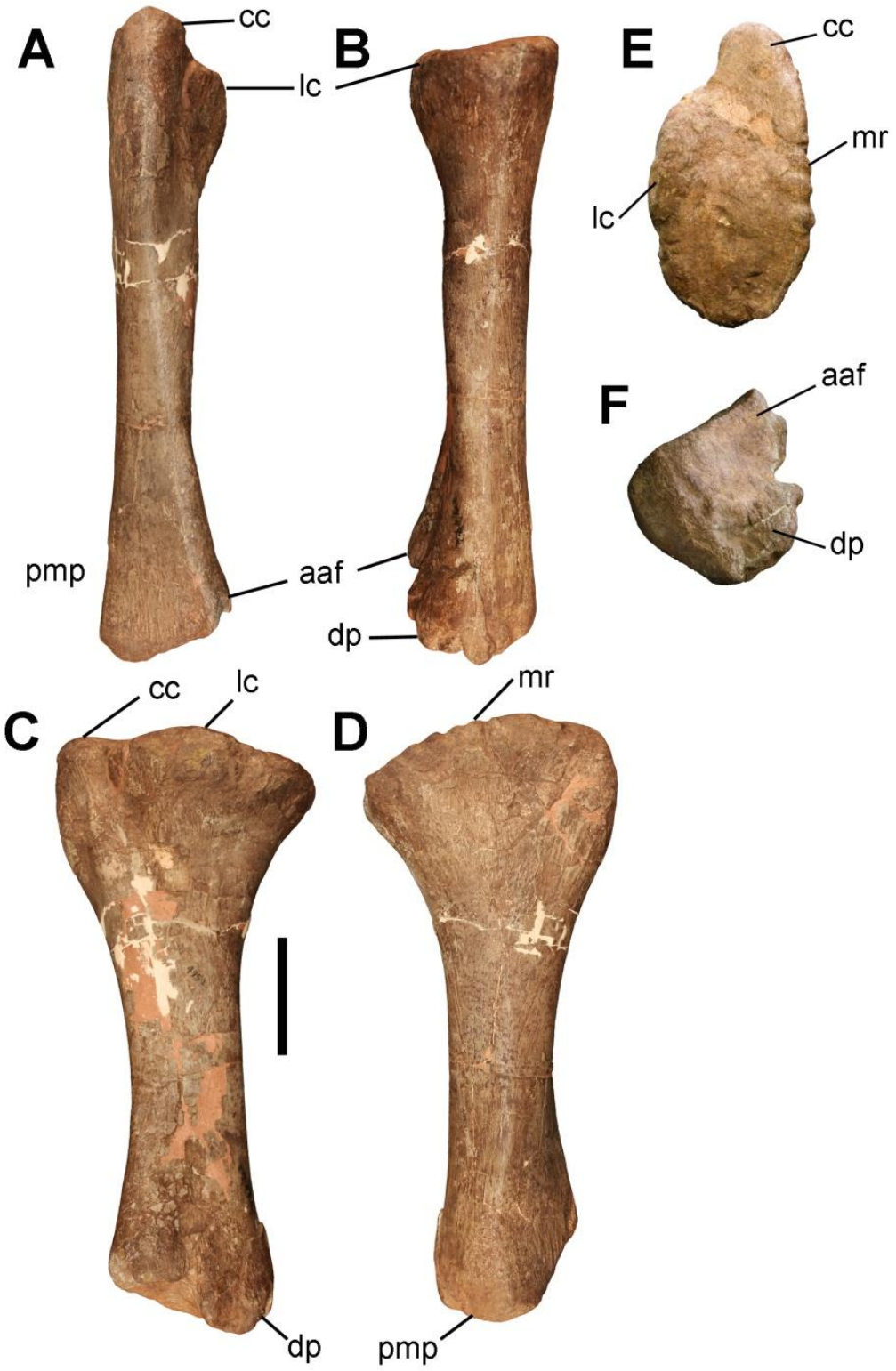

Fig.19. *Antetonitrus ingenipes*, left tibia (BP/1/4952) in **A**, anterior; **B**, posterior; **C**, lateral; **D**, medial; **E**, proximal; **F**, distal views. Abbreviations: aaf, astragalar articular facet (= ascending process); cc, cnemial crest; dp, descending process; lc, lateral condyle; mr, medial ridge; pmp, posteromedial process. Scale bar = 10cm.

4.2.9 TIBIA

The single preserved left tibia is 0.64 the length of the single preserved femur (**Fig.19**). As this is within the range of both derived nonsauropodan sauropodomorphs (e.g. *Anchisaurus*; *Lufengosaurus*; *Melanorosaurus* (NM QR3314)) and sauropod taxa such as *Vulcanodon*; *Mamenchisaurus*; *Apatosaurus*) it is considered highly probable that they belonged to the same individual. The tibia is well-preserved and does not appear to have suffered much (if any) post-depositional distortion.

The tibia is a relatively stout element, being comparable in robustness to those of *Blikanasaurus, Lessemsaurus,* and to the newly described PULR 136 from the Los Colorados formation of Argentina (Ezcurra and Apaldetti 2012), whilst the proximal articular surface is notably similar to that of *Vulcanodon*. As in a number of derived sauropodomorphs (e.g., *Tazoudasaurus*; *Kotasaurus* (115/S1Y/76: Yadagiri, 2001); *Blikanasaurus*) the anteroposterior length of the proximal end of the tibia of *Antetonitrus* is approximately half the total length of the bone.

The proximal articular surface is strongly expanded anterioposteriorly, being over twice the transverse width and thus rendering the proximal surface distinctly elliptical in outline. This feature was described by Allain and Aquesbi (2008) as a synapomorphy shared exclusively with *Tazoudasaurus* and *Vulcanodon*, but also appears to have been present in *Antetonitrus*. Most other non-eusauropod sauropodomorphs (e.g., *Lessemsaurus*, *Melanorosaurus*, *Yunnanosaurus*, PULR 136) have a proximal tibia that is subtriangular in outline, with the transverse width at least 0.60 times the anterolateral depth. The cnemial crest is a stout flange of bone that accounts for 0.25 of the total anteroposterior length of the proximal surface and is mediolaterally wide as it is long. This differs from the mediolaterally broad cnemial crest of *Lessemsaurus* (although it is possible that the flattened morphology observed in *Lessemsaurus* is the result of taphonomic stresses). The degree of lateral deflection of the cnemial crest is very slight, being similar to that seen in *Vulcanodon*. As in *Lessemsaurus* and Sauropoda the cnemial crest does not project dorsally, resulting in a relatively flat proximal articular surface. However, a subtle, posteriorly directed incline can be discerned in the proximal surface of the tibia when viewed laterally in *Antetonitrus*, but this is still considerably less than in *Blikanasaurus* and PURL 136 (Ezcurra and Apaldetti 2012). The proximity of the cnemial crest to the lateral condyle creates a distinct notch (the

'lateral sulcus') that communicates with the anterolateral fossa just below the proximal surface. The anterolateral fossa is irregularly convex and rugose, facilitating as the proximal articulation of the tibia with the fibula. The lateral condyle is a large, rounded protuberance that is situated just posterior to the cnemial crest on the proximal surface of the bone, and is therefore much more anteriorly positioned than the lateral condyle of PURL 136. However, this may be an artefact of the pronounced posterior expansion of the proximal articular surface in *Antetonitrus.* The medial condyle is a slightly more posteriorly placed than the lateral condyle and separated from the latter via a very shallow median depression. Although a much subtler protuberance than the lateral condyle, the medial condyle nonetheless possesses approximately four distinctly rounded tubercles along its proximomedial margin.

The proximomedial surface of the tibial shaft is generally flat and devoid of distinct features. However, a slight concavity, bounded anteriorly by an equally slight rugosity, suggests a site for anchoring musculature (possibly representing the attachment site for the M. gastrocnemius pars medialis [Carrano and Hutchinson 2002]).

Distal to the proximal third of the tibia the medial and lateral surfaces of the shaft are relatively flat, the lateral surface lacking the vertical tuberosity seen in some of the more basal sauropodomorphs (Ezcurra and Apaldetti 2012). The shaft is sub-elliptical in cross-section with the transverse width 0.73 times that of the anteroposterior depth, a substantially greater value than that presented by the mediolaterally constricted tibial shafts of *Vulcanodon* and *Tazoudasaurus*. The distal end of the shaft displays a strong mediolateral expansion, being greater than the transverse width of the proximal end. This condition is observed in a number of derived forms (e.g. *Tazoudasaurus*, *Vulcanodon* and *Lessemsaurus*) but is also seen, to a lesser degree, in more primitive forms such as *Massospondylus, Lufengosaurus* and *Yunnanosaurus*. In contrast, the anteroposterior length of the distal end is less pronounced, being only 0.59 of the anteroposterior length of the proximal end. *Antetonitrus* therefore lacks the pronounced anteroposterior expansion of the distal tibia seen in one of the specimens referred to *Lessemsaurus* (although the tibiae of *Lessemsaurus* appear to have experienced extreme post-depositional distortion, given their rather compacted appearance and the lack of concordance exhibited between the distal ends of both specimens [pers. obs. PVL 4822/66-67]). The proportional relationships

of the distal tibia of *Antetonitrus* are difficult to explicitly define, given the anterolaterally oblique orientation of astragalar ascending facet. This differs from the more mediolaterally oriented distal articular surfaces of most sauropodomorph tibiae (i.e. *Massospondylus*; *Lufengosaurus*; *Melanorosaurus*; *Vulcanodon*), and renders the anteroposterior and mediolateral dimensions of the distal tibia in *Antetonitrus* roughly subequal to one-another. Nonetheless, the distal surface of the tibia can probably be said to be slightly more expanded mediolaterally than anteroposteriorly – as is generally typical of Sauropodomorpha.

The distal articular surface of the tibia is subtriangular in shape, with the tip of the facet for the ascending process of the astragulus (FAA) providing the anterolaterally directed apex of this triangle. As in PURL 136 the (antero)medial and lateral sides of the distal articular surface are sub-equal in length. The FAA is an oblique facet that occupies the anterolateral third of the distal articular surface before gradually sloping distally to meet the posterolateral process and the gently convex mediodistal surface. There is a distinct notch on the lateral surface separating the FAA from the posterolateral process, but this is greatly reduced compared to most non-sauropodan sauropodomorphs (i.e. *Riojasaurus*; *Coloradosaurus*; *Massospondylus*). As in PURL 136, this notch communicates with a very shallow concavity on the distal articular surface, further separating the FAA and the poserolateral process laterally. As opposed to most basal sauropodomorphs, the posterolateral process is transversely compressed and therefore does not exceed the lateral extent of the FAA, rendering the astragalar articular socket visible in posterior view. In recent years this has become an accepted synapomorphy of Sauropoda (Yates 2004; Pol and Powell 2007), being present in *Lessemsaurus*, PURL 136 and more derived sauropod taxa (interestingly also apparent in the gracile early Jurassic sauropodomorph *Anchisaurus polyzelus*: Yates 2004). There is no clear notch on the posteriomedial corner (described as the articular facet for reception of the posteromedial dorsal expansion of the astragalar body) as in PURL 136 and *Riojasaurus,* and also usually present in basal theropods and sauropodomorphs (Ezcurra and Apaldetti 2012). However, a distinct convex notch is present on the posterior corner of the posterolateral process but this is assumed to represent damage to the bone. The anteromedial and posteromedial borders of the distal end are gently concave and gently convex, respectively, the resultant angle between them is acute.

4.2.10 FIBULA

There are two fibulae (**Fig. 20**). The largest, a left, is sub-equal in size to the tibia and possibly belongs to the same individual. The smaller right fibula, while similarly robust, displays some noticeable differences when compared to the larger left fibula. The shaft is bowed and subcircular in the smaller specimen, as opposed to the straight and elliptical shaft of the larger specimen. Another potential difference is that the distal end is twisted and less expanded relative to the proximal end in the smaller specimen. However, as the distal end is damaged and incomplete in the smaller fibula, this interpretation should be treated with caution. These differences may in all likelihood be the product of intraspecific variation, taphonomic influences and/or differential ontogenetic development, but the possibility that these fibulae represent different taxa cannot however be ruled out. Interestingly, a similar relationship is seen between two similarly proportioned fibulae (BP/1/6316 and an uncatalogued element) recovered from the *Aardonyx* type locality, as well as the partial fibulae contained within the NM QR 1545 *Antetonitrus* assemblage, adding some weight to the suggestion that the differences between the two fibulae of *Antetonitrus* are attributable to ontogeny or individual variation.

The following description will focus on the larger, more complete fibula. As in practically all sauropodomorphs the proximal head of the fibula in *Antetonitrus* is considerably longer anteroposteriorly than mediolaterally wide, with a convex proximal outline. The posterior expansion of the proximal head is slightly greater than that of the anterior margin, giving the proximal end a vague hatchet shape in lateral view. However, this could be the result of damage sustained by the anteroproximal margin of the bone. The same damage makes it difficult to confirm if *Antetonitrus* displayed a similar anterior trochanter to that seen in the fibulae of *Vulcanodon* and *Tazoudasaurus*. There is a slight depression on the anterior face of the bone just proximal to mid shaft, a feature that is also clearly present in both the NM QR1545 *Antetonitrus* fibulae and *Plateosaurus* (von Heune 1926) and likely related to the insertion of M. iliofibularis (one of the major flexors of the knee). However, it is unknown whether this process is homologous with the much more proximally placed anterior trochanters of the basal sauropods *Vulcanodon* and *Tazoudasaurus*.

The relatively flat proximal end of the medial surface of the fibula in *Antetonitrus* is marked by the same broad, triangular arrangement of striations – for articulation with the proximal tibia – common to all sauropodomorphs. Anteriorly, the proximal end of the medial surface houses a distinct rugose boss that can also be seen in the smaller fibula (as well as in *Melanorosaurus readi* and *Aardonyx celestae*). The shaft tapers softly from the proximal end with a barely perceptible rise present just above mid shaft on the lateral side. This is substantially subtler than the distinct trochanter visible on the lateral shaft of the fibula in *Tazoudasaurus* and more derived sauropods (described as the origin of the M. flexor digitorium longus: Borsuk-Bialynicka 1977; Wilson and Sereno 1998). The fibular shaft in *Antetonitrus* is straight and elliptical in cross-section with the lateral side softly convex and the medial side softly concave. This contrasts with the condition in a number of non-eusauropodan sauropodomorphs (e.g., *Blikanasaurus*; *Aardonyx*; *Massospondylus; Riojasaurus*) that tend to have medially bowed, subcircular shafts, and is more similar to the derived sauropodan condition (Upchurch et al. 2004). Towards the distal end the anterior margin of the shaft thins, forming a low, axially oriented ridge that is possibly homologous to the vertical crest described for *Tazoudasaurus*. A similar vertical ridge can be seen in the fibula of *Plateosaurus* (von Huene 1926). The distal end expands in the same anteroposterior plane as the proximal end, failing to display the 40-50 degree axial twist of most non-sauropodan sauropodomorph taxa (e.g., *Plateosaurus*; *Yunnanosaurs*; *Massospondylus*). The lack of axial twisting, as well as a distal end that displays a similar degree of expansion as the proximal end, is similar to that of most sauropod taxa (e.g., *Tazoudasurus*; *Spinophorosaurus*; *Barapasaurus*). As in *Melanorosaurus* (Galton et al. 2005) there is an anteromedial sulcus proximal to the distal articular surface that is confluent with an oblique groove that rises from the posteromedial corner of the distal surface. However, as the majority of the distal condyle appears to have displaced laterally due to taphanomic deformation, it is possible that the extent of this rather deep groove may be artificially exaggerated. The distal condyle is flat-to-convex throughout its length and lacking the pronounced posteroventral extension visible in *Blikanasaurus* (Galton and van Heerden 1998).

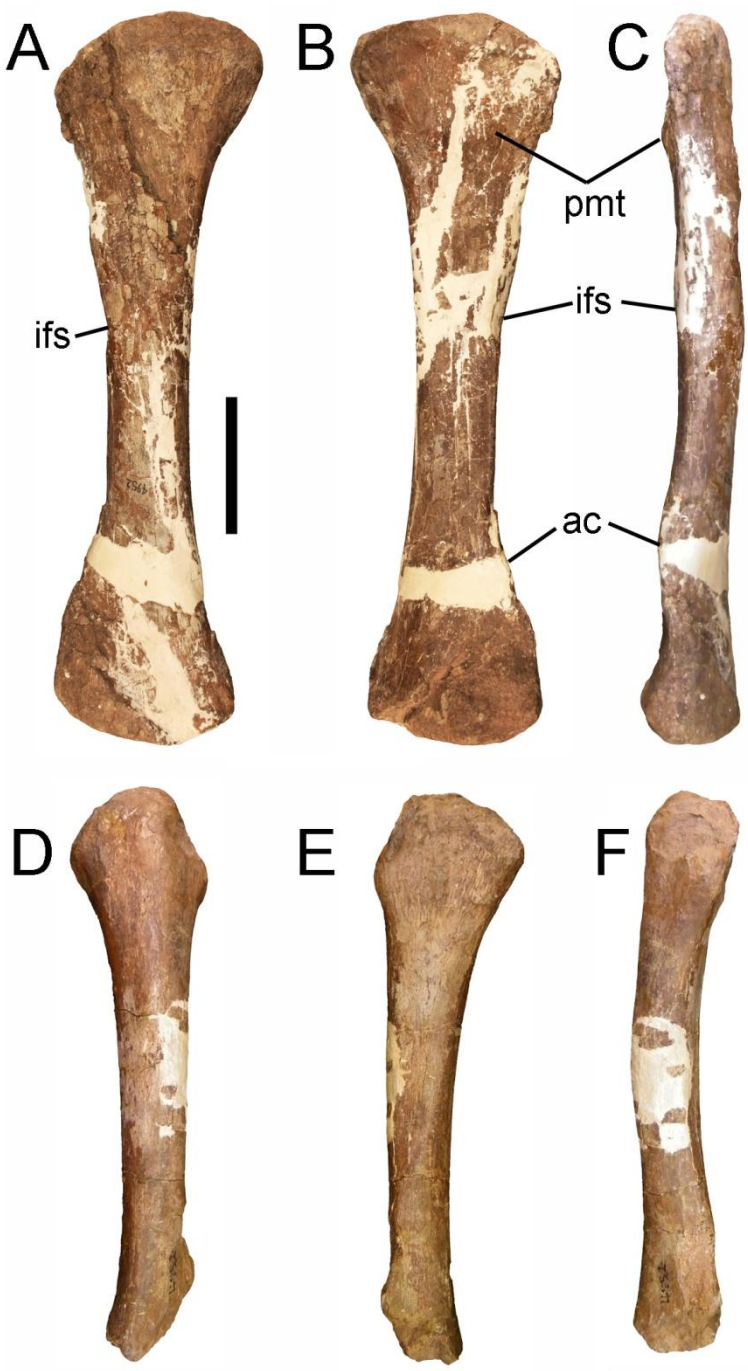

Fig.20. *Antetonitrus ingenipes*. **A**-**C**: left fibula (BP/1/4952) in **A**, lateral; **B**, medial; **C**, anterior views. **D**-**F**: right fibula (BP/1/4952b) in **D**, lateral; **E,** medial; **F**, anterior. Abbreviations: ac, anterior crest; ifs, iliofibularis scar; pmt, proximomedial tubercle. Scale bar = 10 cm.

4.2.11 PES

The pedal elements are represented by a left metatarsal I, a right metatarsal II, a left metatarsal III, a right(?) metatarsal V, two non-terminal pedal phalanges, a right pedal ungual I, and a smaller pedal ungual from possibly the second or third digit. Nearly all the elements are complete, although the distal end of the fifth metatarsal is missing. The metatarsals are also in general proportion (for non-eusauropodan sauropodomorphs) to one another so it is therefore possible they all derive from a single individual. In the original *Antetonitrus* study (Yates and Kitching 2003) a second, smaller metatarsal II was attributed to the 'paratype individual', but this bone cannot currently be located.

The pes is of special interest as it documents the general shortening of the individual elements and, perhaps more importantly, the reduction of the third metatarsal in relation to the first as the weight bearing axis of the foot shifts from mesaxonic to entaxonic at the base of Sauropoda (Carrano 2005).

First metatarsal: The first metatarsal is a squat, robust element most similar in basic morphology to that of *Blikanasaurus* (BPI/1/527/a: Yates 2008), although it is volumetrically larger than the first metatarsal in that species (**Fig.21**). The maximum transverse width (measured as the maximum width of proximal articular surface) of metatarsal I is 0.77 of the total proximodistal length of the bone. This ratio is similar to that of both basal and near-sauropods such as *Blikanasaurus* (0.80), *Aardonyx* (0.74) and *Jingshanosaurus* (Yates 2008). In contrast, most basal sauropodomorph taxa (e.g., *Massospondylus*; *Plateosaurus*; *Leonerasaurus*) display a proportionally longer, more slender first metatarsal with a width/length ratio of around 0.35 - 0.44. An interesting phenomenon, rarely noted upon within the literature, is the tendency for metatarsal I to lengthen again within Vulcanodontidae, with the proximal width/total length ratio of the first metatarsal in *Vulcanodon* and *Tazoudasaurus* approximately 0.62 and 0.52, respectively. In eusauropod taxa such as *Shunosaurus lii* and *Omeisaurus* the first metatarsal has reassumed a squat and robust morphology similar to the proportions observed in *Antetonitrus* and *Blikanasaurus*. This pattern implies a complicated series of evolutionary reversals, the adaptive function/significance of which is unknown. Curiously, the elongated metatarsal I of *Lessemsaurus* appears to present a ratio closer to 'core prosauropods' than that of *Antetonitrus* and *Blikanasaurus*, but examination of Text-Fig. 12 in Pol And Powell (2007)

reveals a first metatarsal that is distinctly atypical in appearance, suggesting either erroneous assignment or diagnosis. Unfortunately, this element could not be located during a trip to the collections at the Instituto Miguel Lillo (PVL), so the curious morphology of the mtI in *Lessemsaurus* could not be investigated further.

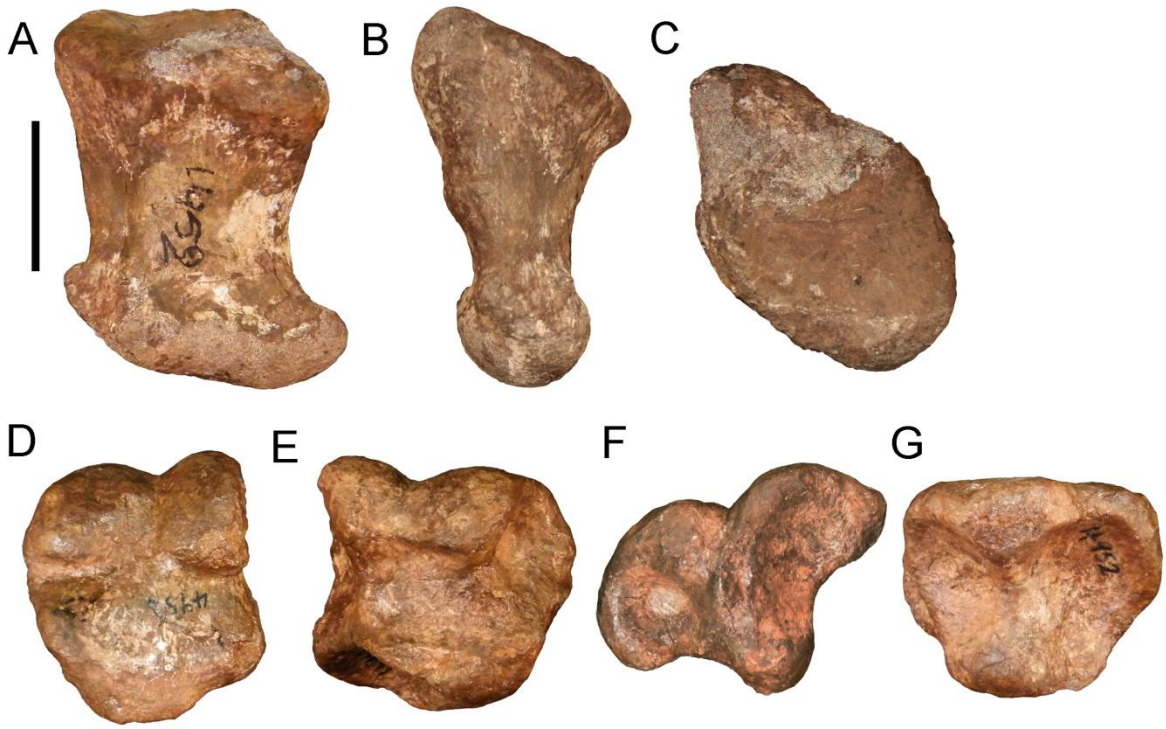

Fig.21. *Antetonitrus ingenipes* (BP/1/4952). **A**-**C**: left metatarsal I in **A**, dorsal; **B**, medial; **C**, proximal views. **D**-**G**: ?right non-terminal pedal phalanx in **D**, dorsal; **E**, ventral; **F**, medial; **G**, proximal. Scale bar = 5cm.

The proximal surface of the first metatarsal in *Antetonitrus* is flat, dorsoventrally deep and ovoid in shape, being subequal in size to the proximal surface of the only preserved metatarsal II. There is a narrow, rounded, protrusion extending from the lateral side of the dorsal surface where it would have overlapped the second metatarsal. This morphology is extremely similar to the proximal articular surface of the first metatarsal in both *Blikanasaurus* and *Vulcanodon*. In contrast, most non-sauropodan sauropodomorphs (e.g., *Massospondylus*; *Plateosaurus*; *Lufengosaurus*; *Aardonyx*) have much narrower proximal heads that are substantially smaller relative to the proximal articular surface of the second metacarpal. The proximal surface is twisted about 40 degrees relative to the transverse axis of the shaft (seen also in *Blikanasaurus* and *Vulcanodon*) and angled so that the articular facet can be seen in anterior view. As noted by Pol et al. (2011), an obliquely oriented

articular facet (when viewed either anteriorly or laterally) has been regarded as a synapomorphy of Eusauropoda (Wilson 2002), but is also clearly observable in *Antetonitrus* and *Tazoudasurus*. In contrast, the proximal articular surface of metatarsal I in most non-sauropodan sauropodomorphs is orthogonal with respect to the proximodistal axis of the metatarsal shaft.

The shaft is markedly short, with its minimum transverse width 0.53 of total bone length. This differs from most basal sauropodomorphs (e.g., *Anchisaurus polyzelus*, YPM 208; *Lufenfosaurus huenei*, LV 003; *Plateosaurus*, von Heune 1926) that display a minimum midshaft width of between 0.21 – 0.31 total length, and is almost identical to the same ratio in the first metatarsal of *Blikanasaurus* and *Omeisaurus tianfuensis* (He et al. 1998). However, it is again stouter than the 0.32 - 0.35 ratio observed within Vulcanodontidae. As in most derived sauropodomorphs the shaft of metatarsal I is significantly thicker than the shaft of metatarsal III, a feature to which *Lessemsaurus* appears to represent a curious exception (but see above).

The distal condyles conform to the typical asymmetrical morphology of derived sauropodomorphs in which the lateral condyle is substantially more developed both dorsoventrally and distially than the medial condyle. There is a well-developed and deep ligament pit on the lateral side of the lateral condyle.

Second metatarsal: The second metatarsal is 1.47 times the length of the first metatarsal. Provided that both the elements derive from a single individual then this ratio is similar, if not slightly reduced, to that of most non-sauropodan sauropodomorphs.

In accord with all the other bones of the pes, the second metatarsal records the shift towards a shorter, more robust foot architecture in sauropod (or near-sauropod) dinosaurs. The maximum transverse width of the proximal surface of the second metatarsal (**Fig.22**) in *Antetonitrus* (measured as total proximal surface visible when viewed anteriorly) is approximately half the proximodistal length of the bone. This proportion most closely matches the second metatarsals of derived sauropodomorphs like *Aardonyx* and *Tazoudasaurus* (Allain and Aquesbi 2008; Yates et al. 2010). In contrast, most basal

sauropodomorphs (e.g. *Massospondylus*, BP/1/4377; *Plateosaurus*: von Heune 1926; *Lufengosaurus*; *Anchisaurus*) have a much more slender second metatarsal, with a maximum width approximately 0.29 – 0.43 times the total length (interestingly, the most basal 'true' sauropod, *Vulcanodon,* has a second metatarsal width/length value that falls between these two groups). In Eusauropda the second metatarsal becomes even squatter, with species such as *Omeisaurus tianfuensis* exhibiting a ratio of about 0.73 (He et al. 1988).

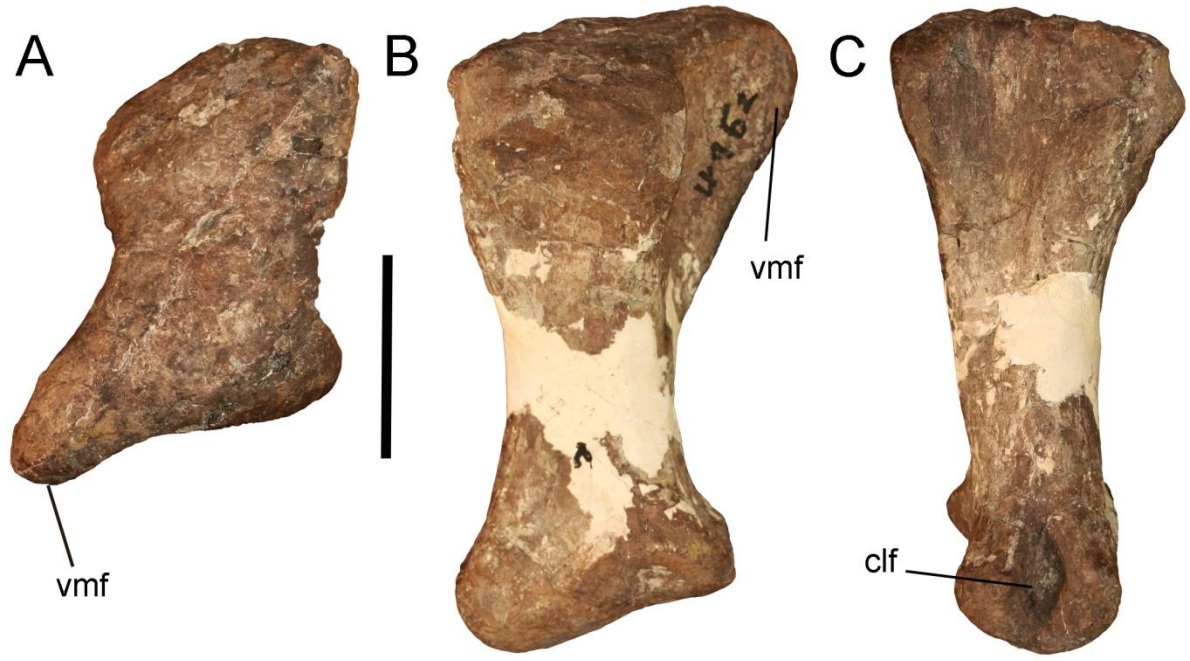

Fig. 22. *Antetonitrus ingenipes,* right metatarsal II (BP/1/4952) in **A**, proximal; **B**, dorsal; **C**, lateral views. Abbreviations: clf, collateral fossa; vmf, ventromedial flange. Scale bar = 5 cm.

Proximally, the articular surface of the metatarsal II in *Antetonitrus* adheres to the well-known bi-concave (or 'hour-glass') morphology recognised in all basal sauropodomorphs (e.g., *Pantydraco*; *Massospondylus*; *Lufengosaurus*), although the medial surface is considerably deeper than the lateral. This morphology reflects the tight articulation of the second metatarsal with the first (medially) and the second (laterally) and appears to have been reduced in *Vulcanodon* and lost in more derived sauropods, although *Tazoudasurus* appears to have retained the plesiomorphic condition (Allain and Aquesbi 2008: Text Fig. 32H). The proximal surface is deeper dorsoventrally than transversely wide and distinctly asymmetrical, mainly on account of the marked expansion of the medioventral corner of the proximal surface (incorrectly described as a 'ventrolateral wing' in Smith and Pol (2007)).

This ventromedial flange of bone likely buttressed the first metatarsal ventrally (possibly reflecting the increased weight-supporting function of that element) and can also be seen in the second metatarsals of other derived sauropodomorphs (e.g. *Aardonyx*; *Vulcanodon*; *Tazoudasaurus*). In contrast, several other non−eusauropod sauropodomorphs have a more developed ventrolateral flange of the proximal surface of metatarsal II (e.g. *Massospondylus*; *Glacialisaurus; Lufengosaurus*).

The shaft of metatarsal II is short and straight with a rhomboidal cross-section. The distal condyles more equally developed than in metatarsal I, although the lateral condyle is still more distally and mediolaterally expanded than the medial condyle, as in most non-eusauropod sauropodomorphs. There is a deep collateral fossa on the lateral surface of the lateral condyle, as on metatarsal I.

Third metatarsal: As in all non-neosauropodan sauropodomorphs the third metatarsal (**Fig. 23**) is the longest element of the pes (although metatarsal IV is not represented here in *Antetonitrus*). The ratio of the length of metatarsal I to metatarsal III in Antetonitrus is 0.58, which is within the immediate range of most other non-eusauropodan sauropodomorphs (e.g. *Plateosaurus*; *Riojasaurus*; *Massospondylus*, BP/1/4377; *Aardonyx*; *Blikanasaurus*). *Vulcanodon*, with its secondarily elongated first metatarsal, displays a higher ratio of ~0.65 (Cooper 1984), and *Lessemsaurus* is more atypical yet, with an mtI/mtIII ratio of 0.79 (Pol and Powell 2007). Pol and Powell (2007:237) state that although the ratio of metatarsal I to metatarsal III in *Lessemsaurus* has no non-eusauropodan correlate, derived forms such as *Omeisaurus maoianus* "have a metatarsal I that is enlarged and similar to that of *Lessemsaurus*." However, examination of the *Omeisaurus maoianus* metatarsus (Tang et al. 2001: fig. 42A) yields a ratio of only about 0.6. Furthermore, although other derived eusauropod forms such as *Shunosaurus lii* and *Omeisaurus tianfuensis* may have had first metatarsals that were proportionately longer when compared to metatarsal III, it is more likely that this is the result of reduction in metatarsal III than enlargement in metatarsal I. This is evidenced by a metatarsal I in *Antetonitrus* that is of similarly squat proportions to those of *Shunosaurus* and *Omeisaurus* and a metatarsal III that displays proportionally shorter (0.43; measured as maximum width of the proximal surface over total proximodistal

length) dimensions than those of most non-sauropodan sauropodomorphs in which a ratio of around 0.24 – 33 is observed (*Anchisaurus*; *Massospodylus*; *Riojasaurus*; *Plateosaurus*). Derived sauropods such as *Shunosaurus lii* and *Omeisaurus tianfuensis* therefore record the further reduction of relative metatarsal III length with proximal width:total length values of around 0.6 (Zhang 1988) and 0.53, respectively.

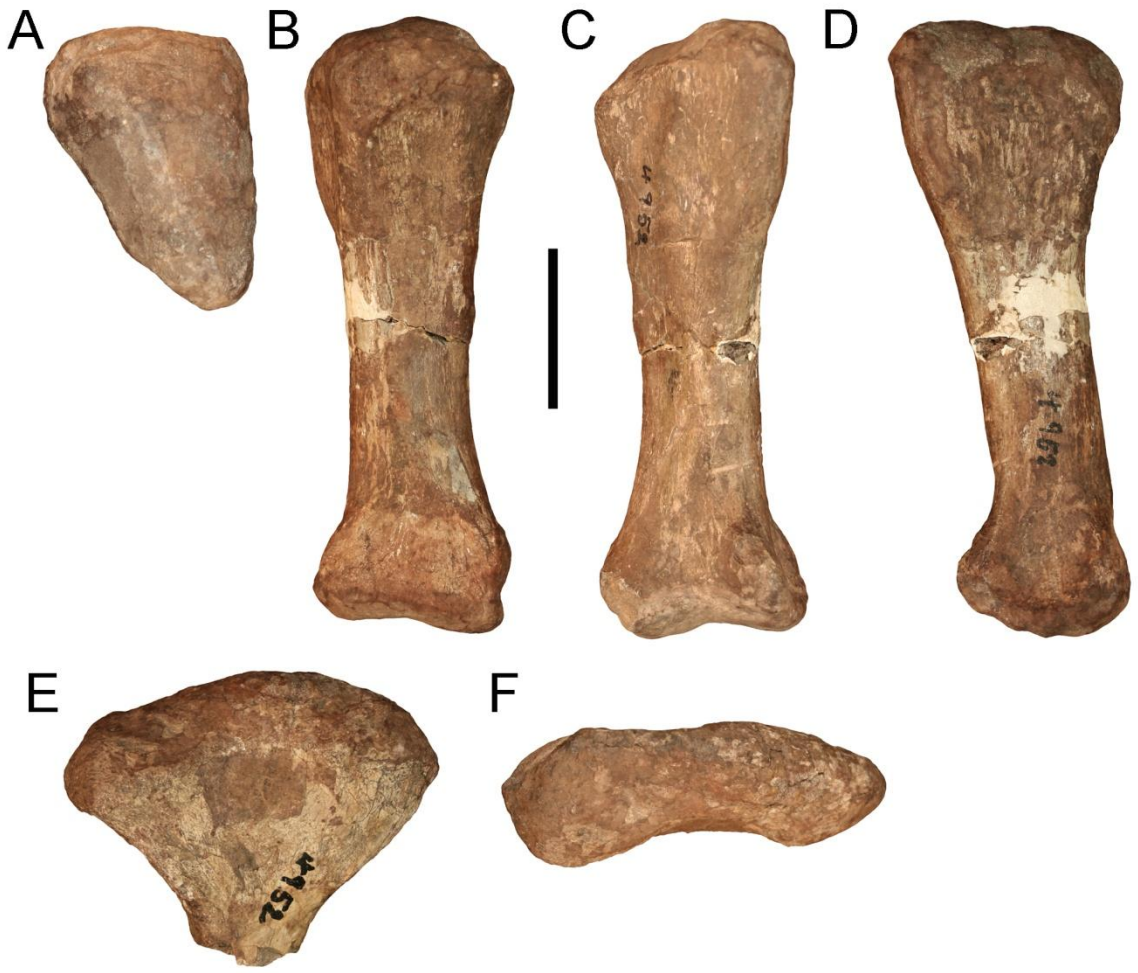

Fig.23. *Antetonitrus ingenipes* (BP/1/4952). **A**-**D**: left metatarsal III in **A**, proximal; **B**, dorsal; **C**, vental; and **D**, medial views. **E**-**F**: ?right metatarsal **V** in **E**, dorsal; **F**, proximal. Scale bar = 5cm.

As is typical of most derived sauropodomorphs (including *Vulcanodon* and *Tazoudasaurus*), the convex proximal surface of the third metatarsal is triangular in outline, with a broad ventrolateral surface and an acute dorsomedial apex. This differs from most massospondylid sauropodomorphs (i.e. *Glacialisaurus; Lufengosaurus; Coloradisaurus*) which have subtrapezoidal proximal outlines in which the posteromedial edge is expanded into a

discrete surface (Smith and Pol 2007). Proximally, on the anterolateral surface of the shaft, there is a faintly striated shallow concavity which potentially represents the insertion area of the M. tibialis anterior (Carrano and Hutchinson 2002; Smith and Pol 2007)

The shaft is straight and subtriangular in cross-section, tapering gently towards the distal condyles which, as in most non-eusauropodan sauropodomorphs, are deflected slightly medially (e.g., *Massospondylus*; *Aardonyx*; *Lessemsaurus*; *Vulcanodon*). On the distal end of the dorsal surface there is another shallow, striated depression which is interpreted as the attachment site for the extensor ligament. The distal condyles are roughly symmetrically developed but the medial condyle is slightly deeper dorsoventrally. On neither the lateral nor medial surfaces of the distal condyles can obvious collateral ligament fossae be observed, but it is possible that the lateral surface still has some adherent matrix obscuring the full dimensions of the fossa.

Fifth metatarsal: Metatarsal V is complete proximally but is missing its distal portion (**Fig. 23**). Although incomplete, it is clear that metatarsal V would have been reduced in much the same manner as in all non-eusauropodan sauropodomorphs. The reduction of the fifth metatarsal in relation to the rest of the pes was traditionally one of the major synapomorphies hypothesised to link a monophyletic 'Prosauropoda' (Cruickshank 1975), however, the transitional state of the fifth metatarsal in derived taxa like *Vulcanodon* and *Omeisaurus* has been pointed out in recent years (Sereno 2007).

As in all non-sauropodan sauropodomorphs metatarsal V in *Antetonitrus* is relatively flat and triangular, displaying the characteristic "paddle" shape common to all basal sauropodomorphs. The convex proximal surface is mediolaterally wide and dorsoventrally shallow, its maximium depth 0.32 of its total transverse width. This is a somewhat smaller ratio than most non-sauropodan sauropodomorphs (e.g. *Massospondylus carinatus*: Cooper 1981; *Plateosaurus engelhardti*, von Huene 1926; *Lufengosaurs huenei*; Young 1941) which have comparatively less transversely expanded fifth metatarsals displaying values of around 0.42 to 45. *Antetonitrus* is therefore closer to the ratios exhibited by *Vulcanodon* (0.36: Cooper 1984) and *Tazoudasaurus* (0.38: Allain and Aquesbi 2008: Text Fig.33D). The dorsal surface is slightly concave and the medial margin is thinner than the lateral margin; this is to be expected as the fourth metatarsal would have overlapped the fifth dorsomedially.

However, the fifth metatarsal in *Antetonitrus* lacks the pronounced medial flange evident in metatarsal V of *Lessemsaurus*. The bone tapers strongly mediolaterally from the proximal surface but, unfortunately, the distal extent of the fifth metatarsal is unknown due to breakage. It is therefore impossible to say if the distal condyle was weakly developed as in all known non-sauropodan sauropodomorphs, or approached the comparatively robust architecture observed in basal sauropods like *Vulcanodon*, *Tazoudasaurus* and *Shunosaurus*.

Pedal phalanges: There are two non-terminal pedal phalanges present (**Fig.21**). Both are markedly robust, with the width of one subequal to its total length and the width of the other rather greater than its length. Given their lack of midpoint constriction and squat morphology, it is likely that they are distal elements, although this represents no more than an educated guess. Given their relatively large size with respect to the metatarsals it is possible that they derive from the inner-digits (potentially II or III), in which case the foot of Antetonitrus can be seen as approaching the short and broad condition seen in eusauropods. However, the pedal phalanges of *Antetonitrus* are plesiomorphic in still retaining strongly developed ginglymoidal articular surfaces and deep collateral fossa (seen also in *Vulcanodon*, *Tazoudasurus* and all non-eusauropodan sauropodomorphs).

Pedal unguals: There are two pedal unguals present in the *Antetonitrus* assemblage. One is a large, well preserved ungual from the right pedal digit I. The other is substantially smaller, less well preserved, and probably belongs to either pedal digit II or III.

Pedal ungual I is longer proximodistally than metatarsal I. Provided that both elements belong to the same individual, this would differentiate *Antetonitrus* from all known non-eusauropodan sauropodomorphs (e.g., *Lamplughsaura*; *Massospondylus; Anchisaurus; Vulcanodon*), which exhibit a proportionally shorter pedal ungual I than metatarsal I. Only in eusauropod taxa such as *Shunosaurus lii* does the ungual of pedal digit I begin to exceed the total length of the first metatarsal. The implications of a greatly lengthened first pedal ungual in *Antetonitrus* at a relatively early stage in sauropodomorph evolution are of undoubted interest; however, as these elements were not found in articulation (and are of

different sides) any presumed association is treated here as tentative. The dorsoventral height of pedal ungual I in *Antetonitrus* is 0.60 the proximodistal length of metatarsal I, very similar to the same ratio in *Lessemsaurus* (Pol and Powell 2007), so it is possible that the pronounced shortening of the first metatarsal in *Antetonitrus* may be contributing to the conspicuous length of the ungual phalanx.

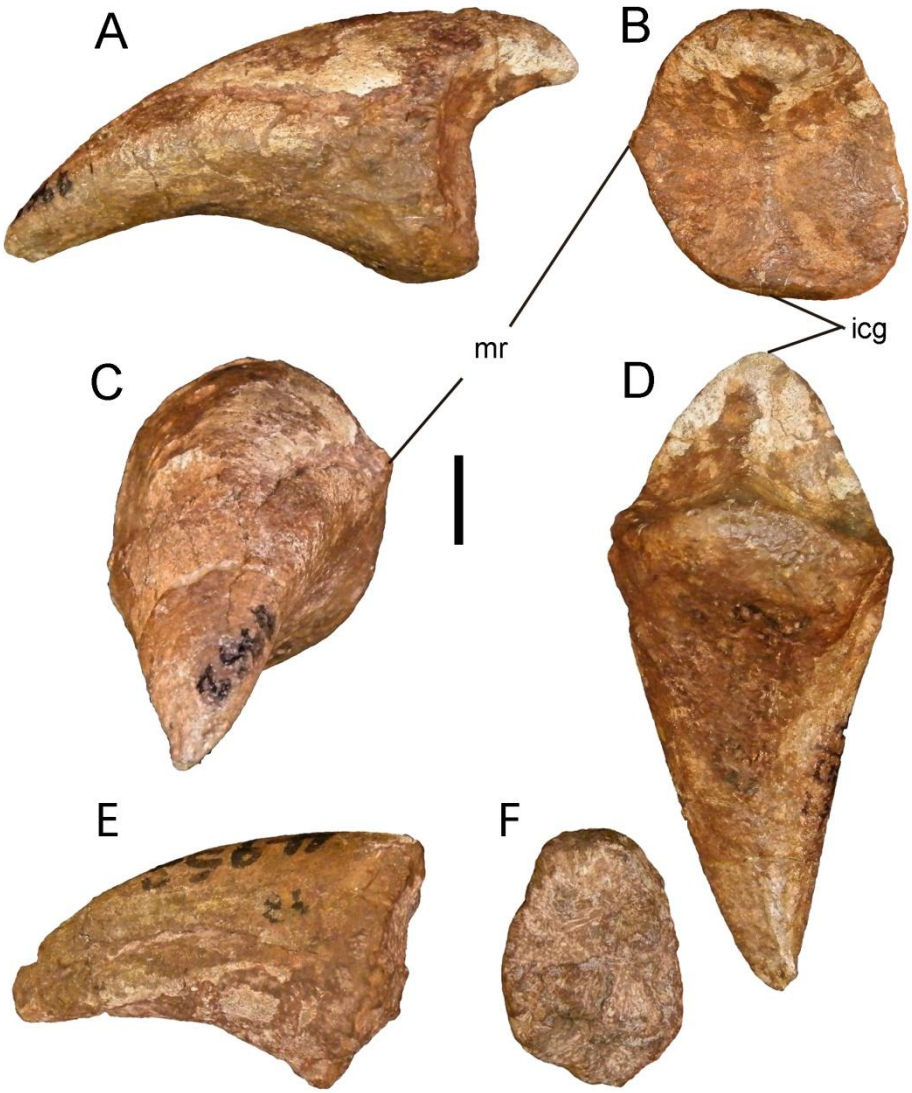

Fig.24. *Antetonitrus ingenipes* (BP/1/4952). A-D: right pedal ungual I, in **A**, medial; **B**, posterior; **C**, anterior; **D**, ventral views. **E**-**F**, pedal ungual ?III in **E**, side-view; **F**, proximal views. Abbreviations: icg, intercondylar groove; mr, medial ridge.

In contrast to *Vulcanodon* and most derived sauropods, the first pedal ungual of *Antetonitrus* is not particularly sickle-shaped or recurved (Bonnan 2005). The proximal articular surface of pedal ungual I is as transversely wide as it is dorsoventrally deep. This

contrasts with most sauropodomorph taxa that tend to have more mediolaterally compressed first unguals (e.g. *Pantydraco*; *Massospondylus*; *Aardonyx; Camarasaurus grandis:* Wilson and Sereno 1998). The two concave proximal articular facets are roughly symmetrical, although the longitudinal inter-condylar ridge is directed obliquely mediodorsally, rendering the medial articular facet somewhat smaller. The proximodorsal lip extends further than the proximoventral base, upon which there is no easily distinguishable flexor tubercle. Pedal ungual I of *Antetonitrus* is laterally deflected along its proximodistal axis so that the convex dorsal surface faces slightly medially and the flatter ventral surface is directed laterally – an orientation further developed in eusauropods (Bonnan 2005). The angle between the dorsal and ventral surfaces is more acute medially than laterally. The lateral and medial nail grooves are shallowly represented and lack the proximal bifurcation of a number of other basal sauropodomorphs (e.g., Massospondylus [BP/1/4377]; Aardonyx [BP/1/7044]), a feature also seen in the largest pedal ungual of *Lessemsaurus* (PVL 4822/78). The tip, although broken at its distal extreme, appears to have tapered to a relatively sharp apex.

Pedal ungual ?III is a smaller, morphologically simpler element that lacks the degree of preservation seen in pedal ungual I. It is mediolaterally narrow, at least relative to the first pedal ungual, lacking the distinctive dorsoventral flattening seen in pedal unguals I and II of *Vulcanodon*. The proximal articular surface is poorly preserved and therefore unable to provide any diagnostic information. There appear to have been very shallow keratin grooves on the mediolateral surfaces. The distal tip is bluntly rounded.

4.3 RESULTS OF CLADISTIC ANALYSIS

The initial cladistic analysis (see Materials and Methods) produced 160 MPT's with a shortest length of 1206 steps. In the strict consensus of this analysis, taxa more derived than *Aardonyx* are grouped as successively unresolved polytomies (i.e. (*Melanorosaurus*, *Blikanasaurus*, *Gongxianosaurus*, *Camelotia*, *Lessemsaurus*, *Antetonitrus*) (*Isanosaurus*,

Vulcanodon, *Tazoudasaurus*)). Additionally, the relationships of all basal saurischians, including the basal sauropodomorphs *Saturnalia* and *Chromogisaurus* remain unresolved.

A posteriori examination of the MPT's reveals that the position of *Camelotia* (in either lacking apomorphies that would place it with higher taxa or possessing conflicting character data) is wildly unstable. The *a priori* pruning of this taxon from the cladistic analysis reduces the number of MPT's to 46 with a best score of 1201 steps. The resulting strict consensus tree is much better resolved, and produces the same basic pattern (with respect to the Massospondylidae and more derived taxa) seen in the phylogenies of Yates (2007a,b, 2010), Apaldetti et al. (2011) and Novas et al. (2011). However, the relationships between the Plateosauridae and basal Massopoda (i.e. *Riojasaurus*; *Eucnemesaurus*) remain unresolved; as do the relationships of basal Saurischia. Additionally, as in the previous analysis the strict consensus tree clusters *Yunnanosaurus* within the basal plateosaurian polytomy, whereas the majority rules consensus supports a position for *Yunnanosaurus* apical to the Massospondylidae in 60% of the trees. These polytomies at both the base of Dinosauria and at the plateosaurian/massopodan boundary appear to be novel developments within the current analysis, and could possibly be related to the modifications suggested by Ezcurra (2010), which may have created potential character conflict. This warrants further investigation but is, unfortunately, beyond the scope of this study.

Nonetheless, the base of Sauropodomorpha can be resolved via one of two possible solutions: 1) the removal of the controversial *Guaibasaurus,* which in successive phylogenetic analyses has been resolved as both a basal sauropodomorph (Ezcurra 2010; Novas et al. 2011) and as the sister taxon to Neotheropoda (Yates 2007a,b, 2010; Langer et al. 2010b; Apaldetti et al. 2011) or 2) deletion of character 184 ("Length of the base the proximal caudal neural spines: less than (0) or greater than (1), half the length of the neural arch"), of which the author failed to observe state (0) anywhere within Sauropodomorpha (*contra* Upchurch et al. 2007b) (additionally this character appears to have accumulated inversion errors at some point in the matrices, rendering its coding both confusing and suspect). This latter scenario produces 16 MPT's of 1194 steps and recovers *Guaibasaurus* as the sister taxon to Neotheropoda in the strict consensus tree (**Fig. 25**). This tree will provide the main focus for the following phylogenetic discussion.

Similar to the results published in Apaldetti et al. (2011), the newly described North American form *Seitaad* (Sertich and Loewen 2010) is a sister-taxon to *Jingshanosaurus* in a relatively advanced position between *Yunnanosaurus* and *Anchisaurus*. The overall topology of the strict consensus tree at nodes more basal to *Melanorosaurus* is much the same as in the topologies produced by Yates (2007a,b, 2010) and Apaldetti et al. (2011), in which a monophyletic Plateosauridae and Massospondylidae is recovered. This is to be expected given that very few basal sauropodomorph/massopodan character-states were modified. Taxa more advanced than *Melanorosaurus* adhere to the 'classic' topology in which *Antetonitrus* and *Lessemsaurus* are sister-taxa at the base of Sauropoda *sensu* Yates (2007). *Isanosaurus* is recovered as more derived than *Vulcanodon*, separating the latter from its 'vulcanodontid' (*sensu* Allain and Aquesbi 2008) sister-taxon, *Tazoudasaurus*. This topology would require a redefinition of 'Gravisauria' *sensu* Allain and Aquesbi (2008) if *Vulcanodon* were to remain within that taxonomic unit (but see Yates et al. 2012); however, as 'Gravisauria' is a subjective junior synonym with the traditional Sauropoda *sensu* Salgado et al. (1997), no redefinition is attempted. The position of *Isanosaurus* as more advanced than *Vulcanodon* is suspicious, given the Rhaetian age of the former, and the ?Toarcian age of the latter, and is potentially an artifact of the considerable sum of missing information on *Isanosaurus*.

It should also be noted that *Eoraptor* in the current analysis is recovered as a basal saurischian of equivocal taxonomic affinity (i.e. it is unresolved in a polytomy with both *Chindesaurus* and *Agnosphitys*) *contra* Martinez et al. (2011) who recovered it as a basal sauropodomorph. Future revision of the character data pertaining to *Eoraptor* in the current matrix is therefore certainly warranted.

Bremer support for nodes within sauropodomorpha is generally no higher than 2 (**Fig.25**), although some groups have relatively high bootstrap values (e.g. Sauropoda *sensu* Salgado et al. 1997 = 68%). Although the grouping of *Antetonitrus* and *Lessemsaurus* is consistently recovered in the final analysis, support for this clade (bootstrap = <50%) is nonetheless reduced compared to previous analyses (Yates 2007a,b). This is likely related to changes in the scoring of *Lessemsaurus* in the current analysis that generally tended towards the more conservative, plesiomorphic condition (see Appendix). The *Lessemsaurus*/*Antetonitrus* clade is supported by a number of unambiguous synapomorphies, including: slit-shaped neural

canals on the dorsal neural arches; dorsal neural spines that are transversely expanded towards their dorsal end; a minimum width of the scapula that is greater than 20 percent of its length; the dorsal expansion of the scapula blade equal to the width of the scapular head; and a first metacarpal the proximal width of which is greater than its length. The only unambiguous synapomorphies linking the common ancestor of *Lessemsaurus* and *Antetonitrus* with more advanced sauropodomorphs (*Gonxianosaurus* + Sauropoda) are two features of the astragalus – an element that remains unknown in *Antetonitrus*. A further possible synapomorphy linking *Antetonitrus* and *Lessemsaurus* to later sauropods relates to the length of the deltopectoral crest (no more than 50% the length of the humerus), but this is rendered ambiguous due to the unknown condition of *Blikanasaurus*.

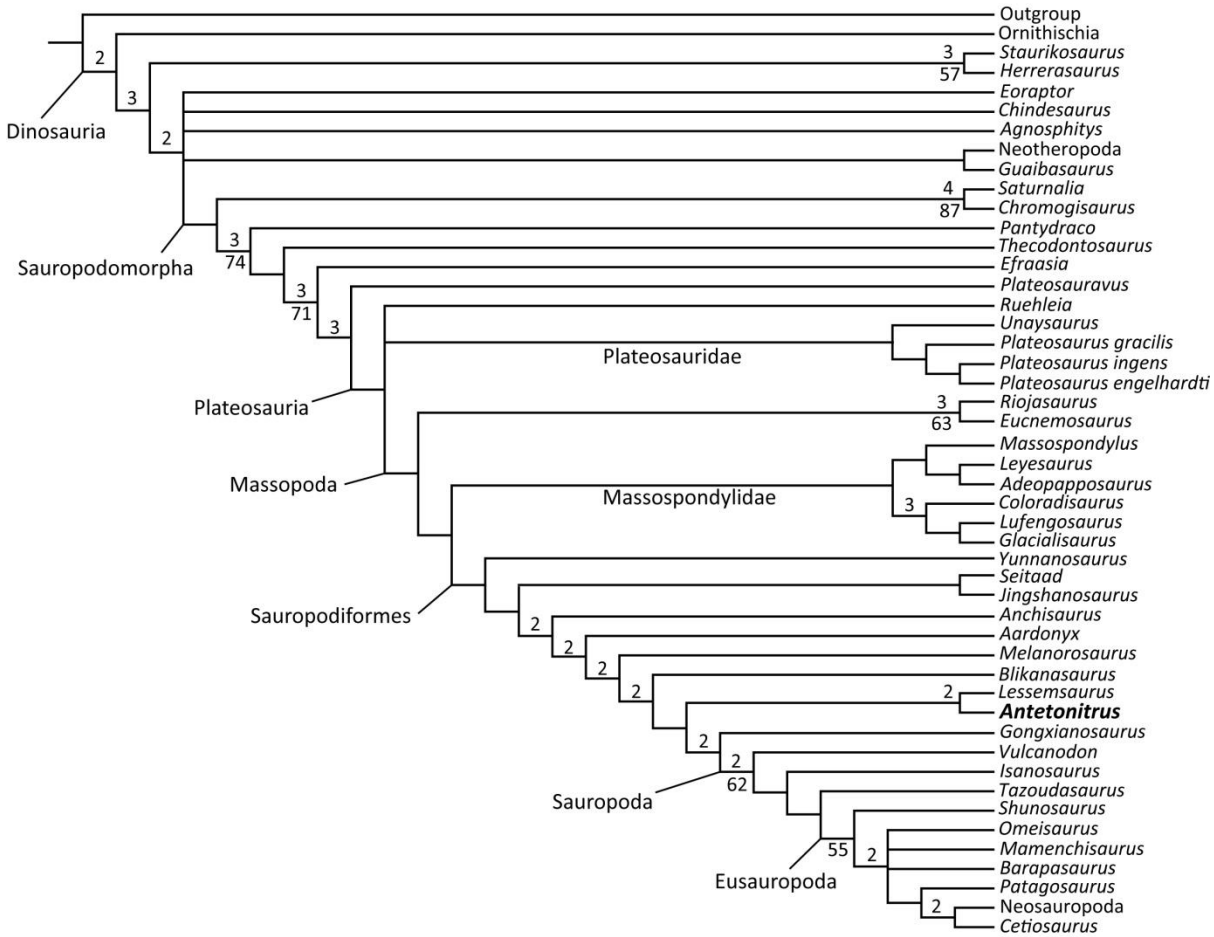

Fig. 25. Strict consensus tree of final cladistic analysis (16 MPTs). Numbers above branches represent Bremer support (>1) and those below represent bootstrap values (>50%).

Sauropoda or Sauropodiformes?

The corroborated position of *Antetonitrus* (even with 30+ character state changes in the current matrix) as a transitional taxon positioned intermediately between a pectinate array of (?bipedal) basal sauropodomorph taxa and the clade of large quadrupedal herbivores of the Jurassic has interesting implications for our understanding of the origins of Sauropoda. In the phylogenetic definition of Sauropoda favoured by Yates (2007a,b), the poorly known *Blikanasaurus* is the only sauropodan taxa more basal than the clade formed by *Lessemsaurus* and *Antetonitrus*, suggesting that these species may present a suite of characters that presage the morphological changes observed in more derived sauropodans. These changes relate to a series of morphological transformations in which a plesiomorphic bauplan that retained a substantial degree of forelimb mobility and manual dexterity underwent the shift towards a specialised form of quadrupedality in which the manus functioned primarily for propulsion during locomotion.

Blikanasaurus + (*Antetonitrus* + *Lessemsaurus*) are linked with more derived sauropods (in Yates' preferred topology) via two unambiguous synapomorphies: the reduction in the length of the third metatarsal relative to the tibia (ch. 336), and the asymmetrically flared ventral surface of the proximal second metatarsal (ch. 354). The former is undoubtedly correlated with the move towards a more graviportal, less cursorial form of locomotion, while the latter also suggests a change in the weight-bearing dynamics of the foot.

Antetonitrus also shares a number of derived characters with Sauropoda that are either non-unique (i.e. appear at nodes basal to *Antetonitrus*) or are rendered as local autapomorphies due to absences in taxa immediately apical to it (although it should be noted that the majority of these 'absences' are exclusive to *Gongxianosaurus*, a taxon for which the available figured information is comparably poor). These include: relatively deep hyposphenes (present from *Melanorosaurus* onwards); invasion of dorsal neural arches by pneumatic diverticula (present to a lesser degree in *Aardonyx* and *Eucnemesaurus*, absent in *Gongxianosaurus* and *Lessemsaurus*); concurrently high neural arches and spines in the dorsal vertebrae (present to a lesser degree from *Aardonyx* onwards, absent in *Gongxianosaurus*); well developed spinopostzygapophyseal laminae (absent in *Gongxianosaurus*); aquisition of a caudosacral vertebra and hyposhenal ridge on anterior

caudals (present from *Melanorosaurus* onwards); anterposteriorly shortened anterior caudal vertebrae (present from *Aardonyx* onwards); a (possibly) elongated humerus (present from *Anchisaurus* onwards); radial fossa on the proximal ulna (also in *Melanorosaurus*); femoral shaft elliptical with reduced sinuosity in lateral view (present to lesser degree from *Aardonyx* onwards); relocation of both the lesser and fourth trochanters (present in varying degrees in both *Aardonyx* and *Melanorosaurus*); an ascending process of the distal tibia that is visible in posterior aspect (present from *Anchisaurus* onwards); and a sloped orientation of the proximal surface of the first metatarsal (absent in *Gongxianosaurus*). From the above it is clear that the paucity of available information on important transitional taxa like *Gongxianosaurus* (*c.f*. He et al. 1998) obscures a detailed reading of the relationships between *Antetonitrus* and taxa immediately apical to it. A comprehensive treatment of this poorly known taxon (and the more robust character data that would result from it) could potentially demonstrate that many of the classically 'sauropodan' characters seen in *Antetonitrus* and more advanced taxa may in fact be synapomorphies of a more inclusive group that includes not only Sauropoda, but more transitional forms like *Melanorosaurus* and *Aardonyx*.

Nonetheless, *Antetonitrus* can be distinguished from the large-bodied, graviportal sauropods of the Jurassic (Sauropoda *sensu* Salgado et al. 1997) by a number of unambiguous synapomorphies present from *Vulcanodon* onwards. These include: the absence of an olecrenon process (?also in *Gongxianosaurus*); deep caudal transverse processes; length of radius greater than 80% the length of the humerus; shortened pubic peduncle of the ilium (inferred from referred material: NM QR1545); reduction of the fourth trochanter to a low, rugose ridge (?also in *Gongxianosaurus*); tibia less than 0.6 times the length of the femur; an enlarged pedal digit V (?present also in *Gongxianosaurus*); a deep, mediolaterally flattened pedal ungual I; and a femur that exceeds 1000mm in size (present also in *Gongxianosaurus*). Clearly, a number of these characters relate to a further specialization of the locomotor apparatus and the accompanying changes in limb (and muscle) dynamics that facilitated both a dramatic increase in size and a quadrupedal gait that favoured power over speed.

The question, therefore, is how similar is the functional anatomy of *Antetonitrus* to Jurassic basal sauropods? Is *Antetonitrus* intermediate in terms of its locomotory apparatus, or is it

functionally equivalent to the earliest fully quadrupedal members of Sauropodomorpha? A number of the character states observed in *Antetonitrus*, especially those of the forelimb, are (for the most part) plesiomorphic for Sauropodomorpha. Discrete features of the humerus (e.g., large, anteriorly projecting deltopectoral creast), antebrachium (e.g., short and robust), and manus (e.g., equally short and robust with a twisted manual digit I) clearly have more in common with the unspecialised form of facultative quadrupedality/bipedality of taxa immediately basal to *Antetonitrus* than they do to the specialised, columnar forelimbs characteristic of Sauropoda *sensu stricto*. However, the hindlimb (and to a lesser degree the axial skeleton) of several taxa on the pectinate line towards *Antetonitrus* indicate the stepwise progression of characters that presage the graviportal bauplan of Sauropoda – a phenomenon that will be explored further in the discussion below.

The name Sauropodiformes is elected here in order to group these 'transitional' forms occupying a contiguous phylogenetic position near the base of Sauropoda. Sauropodiformes in the current analysis is allocated the provisional stem-based definition of all taxa more closely related to *Saltasaurus* than to *Massospondylus*. Sereno (2007) had originally defined Sauropodiformes as 'the least inclusive clade including *Mussaurus* and *Saltasaurus*.' However, *Mussaurus* (at the point of writing) is still a relatively poorly known taxon, whereas the Massospondylidae has been consistently recovered and expanded-upon in the majority of phylogenetic analyses since 2007 (Yates 2007a,b; Apaldetti et al 2011; Novas et al. 2011). Additionally, all the taxa positioned apically to the Massospondylidae in the current analysis were regarded as sauropodiforms in Langer et al.'s (2010a) expansion of the label via the concurrent restriction of Sauropoda to the node-based definition initially proposed by Salgado et al. (1997) (in which *Vulcanodon* is the primitive anchor taxon). Given that the position of *Mussaurus* is liable to change with the publication of better-described, adult individuals in the near future, *Massospondylus* is considered the more robust external specifier for Sauropodiformes here. A stem-based definition is also preferred as a number of basal sauropodiform taxa (e.g., *Yunannosaurus*; *Seitaad*) exhibit regular phylogenetic instability. A minimally inclusive definition that necessitates a basal anchor-taxon therefore runs the risk of redundancy as our understanding of basal sauropodiform interrelationships is further refined.

(Incidentally, an alternative strategy would be to expand the definition of Anchisauria *sensu* Galton and Upchurch 2004 (see also Yates 2007a,b). However, clades named for an individual taxon, especially those specifying a pectinate array of transitional taxa, are problematic insofar the eponym (the taxon for which the group is named) may potentially be recovered in a position external to the group in a later analysis. Furthermore, *Anchisaurus* is an uncomfortable eponym for a group characterised by increasing body size and robustness given that it represents a dramatic reversing of this trend)

Sauropodiformes (as redefined above) is diagnosed by several unambiguous synampomorphies in the current analysis: the lack of an elongate median nasal impression (autapomorphically present in *Melanorosaurus*); mesial and distal serrations on the carinae of the maxillary and dentary teeth (absent in posterior teeth of *Aardonyx*); absence of laterally expanded tables at the midlength of the of the dorsal surface of the dorsal neural spines; posterior margin of the middle dorsal neural spines staright in lateral view; sacral rib not significantly narrower than the transverse process of the primordial sacral vertebra (reversed in *Aardonyx*); length of the manus less than 38% of the humerus + radius (reversed in *Anchisaurus*); absence of a posteriorly projecting 'heel' at the end of ischial peduncle of the ilium (convergent absent in some specimens of *Massospondylus*); absence of a well-developed brevis fossa (also in *Lufengosaurus*); rounded posteromedial process of distal tarsal four in proximal aspect; and a proximal first metatarsal that is at least the same width as the second metatarsal (present also in *Lufengosaurus* and *Glacialisaurus*). These last two characters potentially relate to changes in the distribution of weight-bearing forces across the hindquarters at the base of Sauropodiformes.

Of particular interest is the observation that all of the Sauropodiformes taxa (as defined here) that share a shortened manus (ch. 222) roughly correspond with the genera that Remes (2008) describes as exhibiting 'manus type 2' (wide metacarpal I, robust metacarpals II-IV and block-like phalanges) in his comprehensive study of the evolutionary development of the sauropodomorph forelimb. Furthermore, Remes (2008:252) states that the forms sharing this modified manual type typically display (to varying degrees) adaptations for manus pronation in the antebrachium. This lends modest weight to the suggestion that the basal sauropodiform hand represents a functional trade-off between the need to retain manual dexterity and mobility whilst providing an important auxiliary role in resisting large

loading stresses during contact with the substrate. The bifurcated tubercle observed on the ventrolateral corner of the second metacarpal in both *Aardonyx* (BP/1/386) and *Antetonitrus* may relate – as a potential additional supporting mechanism – to this specific locomotory strategy. A further exploration of the hypothesised range of motion in both *Antetonitrus* and similarly derived sauropodomorph taxa is given in the discussion below.

The difference between either Yates' (2007a,b) or Salgado et al.'s (1997) definitions of Sauropoda is subtle, with one of the key distinctions being the placement of *Antetonitrus* (i.e. as either a derived sauropodiform or as one of the basalmost sauropodan genera), and both definitions express the important transitional nature of this genus. However, as will be discussed below, the mode of locomotion in *Antetonitrus* appears to have been more similar to other closely-related sauropodiforms than it was to the columnar-limbed, obligatory quadrupedal Sauropoda. As the group Sauropodiformes coincides with the advent of changes in limb architecture that presage the derived graviportal condition of Sauropoda, and as *Antetonitrus* (along with *Lessemsaurus*) is perhaps the best known exemplar of this transitional condition, its allocation to the former group is considered here to be the more conservative phylogenetic strategy for the time being.

5. DISCUSSION

5.1 JUST HOW QUADRUPEDAL WAS ANTETONITRUS*?*

The primitive dinosauromorphs/dinosauriforms of the Middle Triassic (e.g., *Marasuchus*) are generally reconstructed as small, facultative (or habitual) bipeds with cursorial limbs (Sereno and Arcucci 1994; Langer et al. 2010a). Although the earliest sauropodomorphs (e.g., *Panphagia* [Martinez and Alcober 2009]; *Saturnalia*, *Thecodontosaurus*) appear to have retained a similar body plan, it took a mere 15-20 million years for the first multi-ton herbivores of the Late Triassic to appear (Bonaparte 1972; Langer et al. 2010a; Rauhut et al. 2011). Of particular interest is the manner in which this relatively rapid change occurred, and in recent years the complex biological, ecological and evolutionary influences that facilitated sauropod giganticism have been investigated in a series of watershed studies (Remes 2008; Sander et al. 2011; Klien et al. 2011; Rauhut et al. 2011). *Antetonitrus*, with its early stratigraphic age and derived appendicular proportions, has been of particular significance to this ongoing discussion, and several studies have identified *Antetonitrus* as the earliest known exemplar of the basal sauropod condition (e.g. Yates 2007 a,b; Allain and Aquesbi 2008; Ezcurra and Apaldetti 2011). However, these studies have mostly relied on the previously published data on *Antetonitrus*, and have not critically looked into the internal dynamics of the holotype material.

When *Antetonitrus* was originally described (Yates and Kitching 2003), the elongate length of the forelimb was listed as one of the principal diagnostic features linking *Antetonitrus* with the obligatory quadrupedal sauropods of the Early Jurassic. Explicit in this view was the understanding that the fossil assemblage BP/1/4952 represented no more than two individuals; a sub-adult holotype that collected the majority of the remains and a smaller, more juvenile paratype (Yates and Kitching 2003). However, with reference to the above description, it is clear that such a division no longer accurately reflects the internal dynamics of the *Antetonitrus* fossil assemblage. In terms of a simple MNI count of the entire assemblage, the scapulae alone account for three different individuals (two subequally sized left-sided elements and a substantially smaller right). This, along with the concurrent

duplication of two identically-sized right-sided metacarpals II raises the additional possibility of more than a single individual of similar size being present.

As reconstructed in Remes (2008), it is likely that the larger humerus, ulnae, radius, and manus (at least metacarpal I) represent an individual forelimb. This is supported by agreement in the inter-relationships of each element with the general proportions observed within the majority of derived Sauropodomorpha genera. However, the smaller duplicate elements of the forelimb (humerus and ulna: BP/1/4952b) are harder to configure, and it is less likely that the ulna belongs with the humerus given that the former is 0.7 times the length of the latter (which would be unusually high for a Triassic sauropodomorph) compared to ratio of 0.59 observed in the larger elements (although it is possible that this reflects allometric growth of the forelimbs). If the large, duplicate left-sided metacarpal II and scapula (= BP/1/4952c) are then considered, the number of individuals represented by the pectoral girdle and forelimb alone rises to potentially as many as 4 (see Table 4).

Individual	Scapula	Humerus	Ulna	Radius	McI	McII	Pubis	Femur	Tibia	Fibula	Pes
1	L	R	*	R	R	L					
2	L					L					
3	R	R									
4			R							R	
5							L	L	L	L	

TABLE 4. Appendicular bones present in the *Antetonitrus* type quarry and their hypothesised relationships. Light grey = BP/1/4952, which is split to convey uncertainty in inter-relatedness. Dark grey = BP/1/4952c and mid-tone = BP/1/4952b. Dashed lines also represent uncertainty in hypothesised 'individuality'. R = right; L = left; * = both elements present.

The relationship of the major collection of the forelimb material to the hindlimb material is harder to determine, and is essentially contingent on the relationship of the larger humerus to the femur. If, as originally hypothesised (Yates and Kitching 2003), both elements are collected under the holotype BPI/1/4952 as belonging to a single individual, a dramatic increase in relative humerus-to-femur length (= 0.9) within a relatively limited temporal span must ultimately be postulated. All other sauropodomorphs from the late Triassic for whom the relative humerus-to-femur lengths are known have a humeral/femoral ratio of between approximately 0.53 – 0.78 (e.g. *Plateosaurus; Anchisaurus; Lufengosaurus; Riojasaurus; Melanorosaurus*). In fact, it is not until the advent of later Jurassic species such as *Brachiosaurus* (Riggs 1903; Taylor 2009) that sauropods begin to display a

humeral/femoral ratio of over 0.9 (**Fig.26**). One curious exception may be that of *Yunnanosaurus*, which in a recent analysis of sauropodomorph morphometrics (Rauhut et al. 2011) was described as having a humeral/femoral ratio of 0.96. However, in the original description (Young 1942) this same individual (IVPP V 20) has a humeral/femoral ratio of only 0.53. Unfortunately, the reasons for this rather marked discrepancy are unknown.

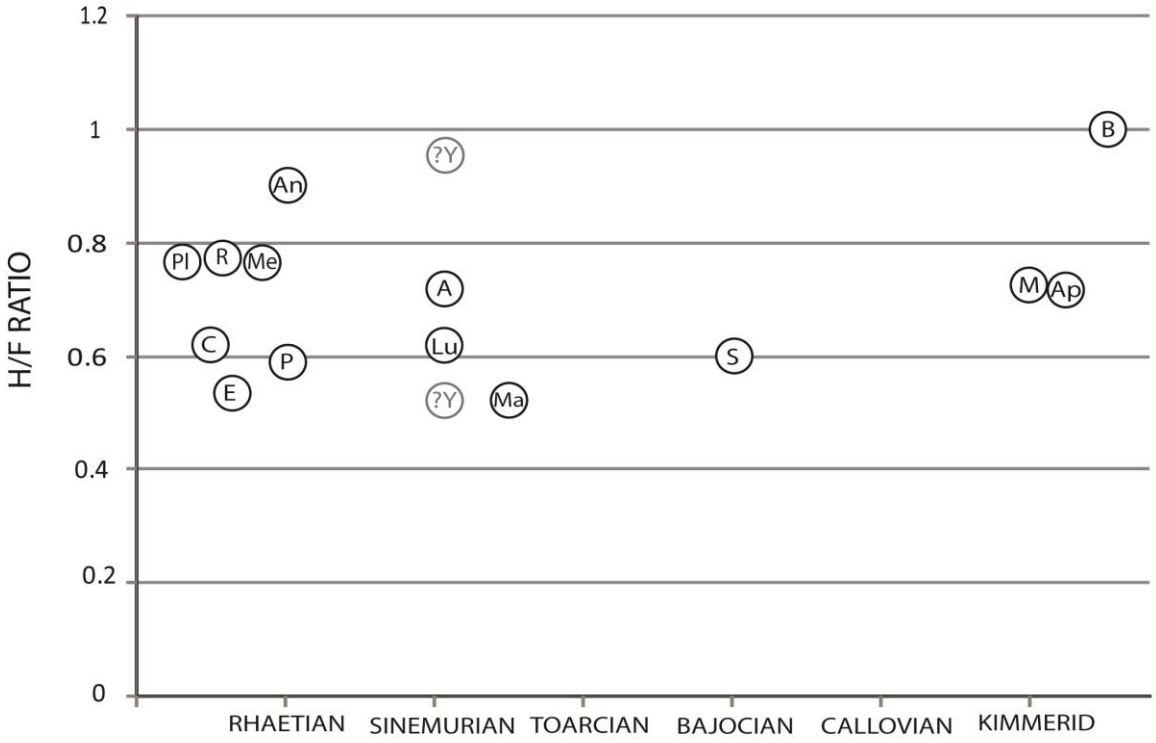

Fig. 26. Sauropodomorph humerus-to-femur ratios by geological age. The dual placement of Y: *Yunnanosaurus* (IVPP V20) indicates the discrepancy in measurements given in Young (1942) and Rauhut et al. (2011). Taxa: A, *Anchisaurus* YPM 1883 (Rauhut et al. 2011); An, *Antetonitrus* BP/1/4952; Ap, *Apatosaurus* (Rauhut et al. 2011); B, *Brachiosaurus altithorax* FMNH P 25107 (Taylor 2009); C, *Coloradisaurus* PVL 5904; *Efraasia* SMNS 12667 (Rauhut et al. 2011); Lu, *Lufengosaurus* IVPP V20 (Young 1941); M, *Memenchisaurus* ZDM 0083 (Rauhut et al. 2011); Ma, *Massospondylus* SAM-K-5135 (Bonnan and Senter 2007); Me, *Melanorosaurus* NM QR3314; P, *Plateosaurus* SMNS13200 (Rauhut et al. 2011); Pl, *Plateosauravus* SAM-K-3342, 3602 (Van Heerden 1979); R, *Riojasaurus* PVL 380; S, *Shunosaurus* ZDM T 5402 (Rauhut et al. 2011).

The referred assemblage NM QR 1545 lends modest support for an elongate humerus in *Antetonitrus* as the assemblage contains a solitary humerus and (mostly) complete femur of almost identical relative (and absolute) lengths to that of the Bernard Price material. However, as the National Museum assemblage also preserves the remains of at least three

differently sized individuals, any supporting evidence has to be regarded with this caveat in mind. Anecdotal evidence for elongation of the humerus is also offered also by Guaffre (1993) in his referral of the 'Bloem dino' to '*Euskelosaurus*' (later renamed '*Kholumolumosaurus*' Gauffre 1996). This material was excavated from Maphutseng in Lesotho between 1955 and 1970 by Ellenberger and represents a massive, potentially mono-specific dinosaur bone-bed that is now divided between Cape Town and Paris (see material and methods). According to Guaffre (1993) this material conforms to the diagnostic criterion of '*Euskelosaurus*' (van Heerden 1979) in which the length of the humerus approaches 80 percent of that of the femur. However, as it is near-impossible to gauge the individuality of various limb bones within what appears to have been a spectacularly large (and abysmally recorded) quarry of dissociated sauropodomorph material, any assumptions of association of elements should be treated with caution.

It should be noted, also, that if the total length of the forelimb (i.e. humerus + radius + mcII) is compared to the total length of the hindlimb (i.e. femur + tibia + mt III) the resulting metric is slightly less extreme with a forelimb/hindlimb ratio of around 0.81. Although this metric is similar to a greater variety of taxa than that of the humerus/femur ratio, it is again shared exclusively with sauropods of the late Jurassic (e.g. *Mamenchisaurus*; *Jobaria*; *Camarasaurus*) while being significantly greater than that of the basal sauropod *Shunosaurus* (0.66; see Rauhut et al 2011: 125). This implies an appendicular specialization in *Antetonitrus* that is in marked contradistinction with the observed phylogenetic trend of Triassic-Jurassic sauropodomorphs. There is an additional danger in extrapolating the length of entire limbs from multiple-individual assemblages as the reliance on a greater number of elements (i.e. three for each limb) can conflate any inaccuracies that may arise in the erroneous assignment of particular limb segments. It is clear, therefore, that the formulation of hypotheses regarding an early evolutionary experiment in quadrupedal high-browsing in *Antetonitrus* will likely have to await the discovery of more complete, semi-articulated specimens.

5.1.1 BEYOND RATIOS: THE RANGE OF MOTION IN ANTETONITRUS *AS INFERRED FROM RECENT STUDIES INTO SAUROPODOMORPH FUNCTIONAL MORPHOLOGY.*

Although the relative lengths of the appendicular (and axial) skeleton exerts an undeniable influence on the locomotory strategies of all tetrapods, a quantitative assessment of the relationship of various limb and trunk ratios to inferred locomotory behaviour in sauropodomorph dinosaurs has proven notoriously difficult to pin down.

Galton (1976, 1990) originally suggested that bipedality in dinosaurs could be inferred if the hindlimb-to-trunk ratio exceeded 1.0. However, Rauhut et al. (2011) have recently pointed out that even advanced neosauropods such as *Camarasaurus* and *Apatosaurus* – both unequivocal quadrupeds - had hindlimb-to-trunk ratios easily exceeding 1.0. The fact that entire vertebral columns are rarely preserved in the fossil record (as is the case with *Antetonitrus*) renders this metric a somewhat problematic proxy for locomotory behaviour in the first place. Additionally, Bonnan and Senter (2007) found no consistent trend between the relative lengths of the humerus and femur (nor of the complete forelimb to the hindlimb) throughout a number of sauropodomorph and sauropod taxa. However, the phylogenetic significance of differential limb disparities is again muddied by conflicting accounts of the length of the forelimb in *Plateosaurus* (SMNS 13200) given in Bonnan and Senter (2007; = 1031mm) and Rauhut et al. (2011; = 740mm).

Nonetheless, Bonnan and Sentor (2007:151) have cautioned that an overreliance of such metrics, independent of functional and phylogenetic data, cannot by themselves elucidate habitual posture and locomotion in sauropodomorph taxa. Investigating the functional anatomy of the forelimb of the well-known 'prosauropod' forms *Plateosaurus* and *Massospondylus,* Bonnan and Sentor (2007) argued that these dinosaurs lacked the requisite adaptations for efficient, habitual quadrupedal locomotion. This was primarily due to the plesiomorphic morphology of the antebrachium that precluded the anterior rotation of the radius about the ulna; hence the manus retained a semi-supinated ('prayer-like') orientation that prevented the hand from producing a posteriorly directed propulsive force that paralleled the foot. This was further corroborated by Mallison's (2010a,b) virtual reconstruction of a complete *Plateosaurus* specimen (GPIT1) in which the digital skeleton

was depicted as an agile, obligate biped with strong grasping hands (see below). The disparity in lengths of the fore- and hindlimb and the restricted range of motion in the forelimb meant that any manner of quadrupedal locomotion would have been particularly difficult in *Plateosaurus* (Mallison 2010a,b).

However, the forelimb in *Plateosaurus* is notably short relative to most sauropodomorph genera, and it is reasonable to expect that the forelimb of at least some derived (i.e. massopodan) taxa exercised a degree of interaction with substrate – either when feeding, resting, or walking at reduced speeds. Accordingly, ichnotaxa such as *Navahopus* and *Tetrasauropus* (and possibly *Otozoum*) indicate that some description of sauropodomorph dinosaur must have employed the forelimb in locomotion from at least the very early Jurassic – if not earlier (Baird 1980; Rainforth 2003; Wilson 2005a; Bonnan and Sereno 2007).

Utilising myological data from both living and extinct sauropodomorph outgroup taxa, Remes (2008) found no major modifications in the early sauropodomorph forelimb that indicated obligate bipedalism (with the exception of *Plateosaurus*), raising the somewhat controversial suggestion that quadrupedalism, not bipedalism, was the primitive locomotory state of dinosaurs (*contra* Novas 1996; Sereno 1999; Benton et al. 2000). Remes (2008) argued that the major modifications of the sauropodomorph forelimb are a functional adaptation towards increased manoeuvrability during feeding (i.e. in facilitating the manipulation of branches and other vegetation). Features associated with this adaptation include the convexly expanded humeral head seen in a number of sauropodomorph species (including *Antetonitrus*), an enlarged deltopectoral crest and its associated muscle attachments (although these appear slightly reduced in *Antetonitrus*), and a hypertrophied forearm flexor (M. biceps brachii).

Remes (2008) also highlights two mutually distinctive strategies for manual pronation in the forearms of several derived sauropodomorphs. These are argued to improve the functionality of the hand as a grasping (and potentially support) structure and involve either the lateral shift of the anterior tubercle of the radius (which would rotate the distal end of the radius anteromedially relative to the ulna during contraction of the M. brachialis), or an oblique course of the long axis of the radial shaft relative to its proximal and distal articular

surfaces (once again placing the distal end of the radius somewhat anteromedial relative to the distal ulna). Remes attributes the latter adaptation to *Antetonitrus* (2008:250) before perplexingly stating that neither strategy can be observed in that taxon (2008:313). Nonetheless, the distal end of the radius in *Antetonitrus* can clearly be seen to be offset at an angle of well less that 90 degrees from the vertical axis of the shaft.

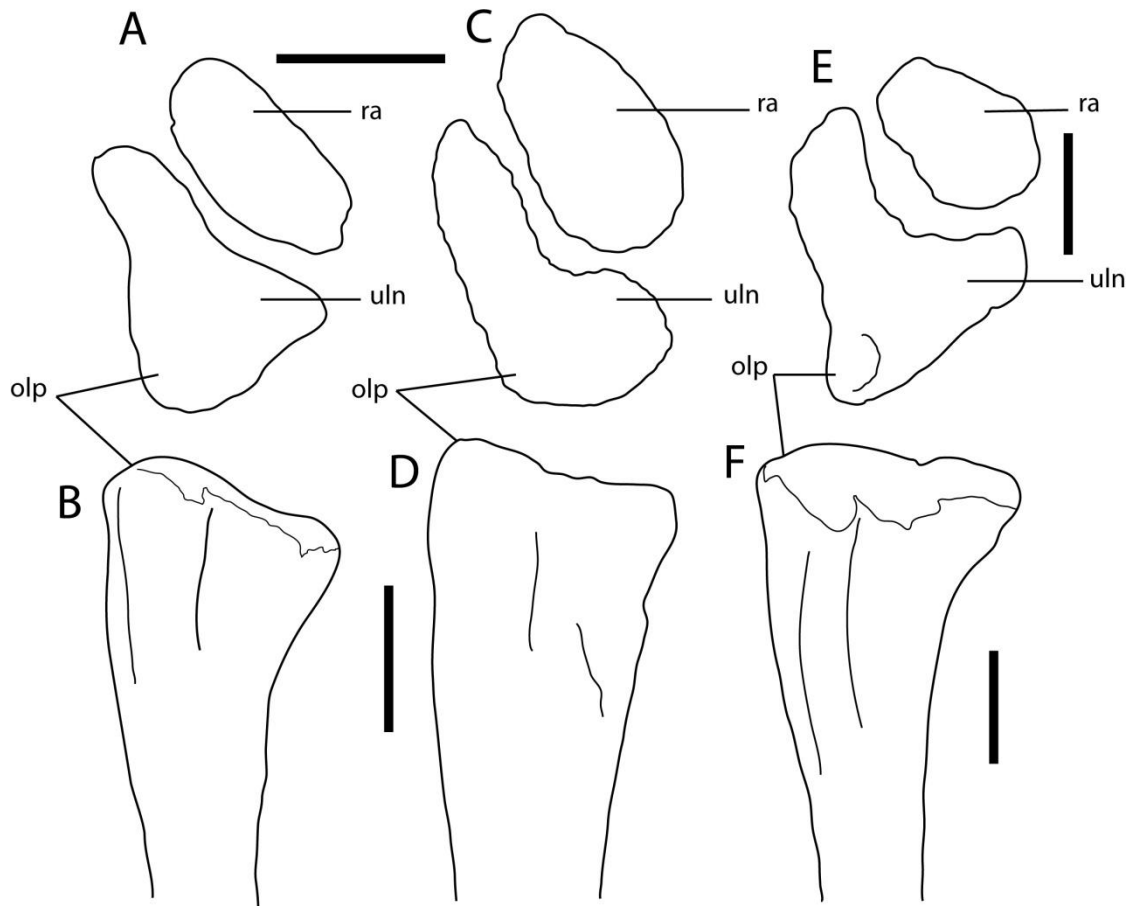

Fig. 27. Changes in radius and ulna morphology throughout Sauropodomorpha. **A**-**B**, *Antetonitrus ingenipes*: **A**, right ulna and radius in proximal view; **B**, right ulna in lateral view. **C**-**D**, *Vulcanodon karibaensis* (modified from Cooper 1984): **C**, right ulna and radius in proximal view; **D**, right ulna in ?lateral view. **E**-**F**, *Camarasaurus grandis* (modified from Wilson and Sereno 1998): **E**, left (reversed) ulna and radius in proximal view: **F**, left (reversed) ulna in lateral view. Abbreviations: olp, olecranon process; ra, radius; uln, ulna. Scale bars = 10cm.

Other features of the forelimb provide a less ambiguous indication of the degree of manual pronation possible in *Antetonitrus*. These features (regularly hypothesised as representing the incipient stages of the sauropod condition) include a reduction in the amount of posterodorsal deflection of the radial condyle of the humerus (and thus a less supinated

hand) and the anterior rotation of the proximal radius around the ulna as enabled by the moderately enlarged lateral process (= radial fossa) of the ulna (see Bonnan 2003; Bonnan and Yates 2007; Bonnan and Sentor 2007; Remes 2008). However, neither of these features are as developed as in later 'true' sauropods or eusauropods (**Fig. 27**), with Remes (2008: 256) concluding that "no basal sauropodomorph, including *Antetonitrus*, exhibits unambiguous adaptations in the skeleto-muscular system that might indicate an improved, parasagittal stance and gait of the forelimb. Instead, the plesiomorphic protraction/retraction system is retained, which inflicts a significant lateral component in the movements of the humerus." The presence of a deep inter-condylar cavity (= cuboid fossa) on the distal humerus, along with the retention of a pronounced olecranon process on the proximal ulna, further suggests that *Antetonitrus* retained the degree of compression-resistant flexion consistent with the partially abducted forelimb posture plesiomorphic to archosaurs (Remes 2008).

As it appears that most non-sauropodan sauropodomorphs would have struggled to protract the humerus beyond a sub-vertical position (Bonnan and Sentor 2007; Remes 2008; Mallison 2010a, b) a semi-abducted forelimb likely represents an important postural stopgap for those advanced forms that exercised some degree of facultative quadrupedalism. A semi-sprawled humerus would have also assisted in the anterior rotation of the manus in basal genera that exhibited only a limited capacity for manual pronation. Nevertheless, while the degree of pronation was relatively restricted in most non-sauropodan sauropodomorphs (including *Antetonitrus*), it should be noted that the fully pronated, tubular manus of neosauropods was primarily an immobile support structure with the majority of propulsive force being generated by the hindlimb (Bonnan 2003; Carrano 2005). Therefore, the semi-supinated manus of 'prosauropods' is more indicative of a retained grasping ability than it is a lack of supportive/propulsive potential. The lengthened, comparatively gracile metacarpals of later sauropod taxa (e.g. *Vulcanodon*; *Tazoudasaurus; Shunosaurus*) can probably be viewed in association with a specialized feeding strategy primarily dedicated to the optimization of features of the neck and skull (and hence a further decrease of the disparity between the fore- and hindlimb). It is possible that features of the *Antetonitrus* humerus (such as a reduced medial tuberosity that is oriented in parallel with the proximally expanded, dome-like humeral head) suggest a more erect, sauropodan

orientation of the humerus. However, as a plesiomorphic sub-perpendicular angle between the long-axes of the scapular blade and head is retained, it is unlikely that the anteroventral rotation of the glenoid seen in sauropods (which permitted a more vertical orientation the humerus) can be ascribed to *Antetonitrus* (see Remes 2008). Unfortunately, as the coracoid remains unknown in *Antetonitrus,* the full range of movement afforded by the glenoid is difficult to surmise.

Features of the forelimb, therefore, are equivocal in elucidating the role that the anterior appendage played in the 'typical' sauropodomorph (or sauropodiform) locomotory repertoire; with most evidence suggesting that *Antetonitrus* retained a number of basal adaptations related to the continued mobility of what was undoubtedly a very important feeding apparatus. The forelimb, however, represents only a single aspect of the total locomotory suite, and one might expect that the majority of characters relating to the reorganisation and distribution of physical mass in Sauropodiformes would be located in the limb most proximate the centre of that mass – the hindlimb.

The hindlimb in both stem (e.g. *Marasuchus*) and basal (e.g. *Eoraptor*; *Herrerasaurus*) dinosaurs has traditionally been characterised as the cursorial extension of an obligate biped (e.g. Charig 1972; Sereno and Arcucci 1994; Novas 1996; Benton et al. 2000). Features such as a medially inturned femoral head and a (semi) perforated acetabulum are often cited as evidence of a parasagittal gait, and hence bipedality when considered in conjunction with the disparity in length of the fore- and hindlimb. It has therefore been an uncontroversial proposition that basal-most sauropodomorphs retained a habitually bipedal posture, and the majority of locomotor reconstructions – especially of 'thecodontosaurids'– have supported this viewpoint (Galton 1976; Galton 1990; Galton and Upchurch 2004; Benton et al. 2000).

Langer (2003) was the first to comprehensively explore the locomotor posture of a (very) basal sauropodomorph (*Saturnalia*) with reference to the functional morphology of the hindlimb. Although *Saturnalia* shared the disparate limb proportions and elongated epipodium of non-dinosaurian dinosauromorphs, the degree of lateral movement inferred from the reconstructed hindlimb (along with the potentially heightened trunk/hindlimb ratio) led Langer (2003) to suggest that quadrupedality constituted an important part of the

Saturnalia behavioural suite. This observation was in general agreement with the hypotheses of Remes (2008) and Fechner (2009), who argued that basal taxa such as *Marasuchus* and *Eoraptor* exhibited an 'intermediate' locomotor posture in which facultative bipedality was practised only when the animal needed to move at high-speeds (a similar phenomenon is seen in some modern lizards). An erect hindlimb, therefore, probably has less to do with bipedality than it does with the retention (and improvement) of cursorial abilities at larger sizes via the channelling of ground-reaction forces through a more vertically oriented limb (e.g. Biewener 1989, 1990, 2005; Christian 2007;Fechner 2009).

In light of the above one may conclude that perhaps no sauropodomorph can be characterised as having been strictly bipedal. Accordingly, the 'bipedal-only-when-running' argument has proven relatively robust, and most reconstructions of the hypothesised range of motion in large-bodied 'prosauropod' dinosaurs have perpetuated this idea (e.g. Wellnhofer 1994; Christian and Preuschoft 1996; Galton and Upchurch 2004). Christian et al. (1996) reconstructed the hindlimb posture of *Plateosaurus* as a more erect version of the sprawling locomotory gait of lizards (as previously suggested by van Heerden (1979, 1997)) based on the large adductor-based attachments of the pelvic girdle. Although this superficially agrees with Langer's (2003) reconstruction of the hindlimb in *Saturnalia*, *Plateosaurus* was a considerably larger animal, and a semi-sprawled hindlimb is at distinct odds with the bipedal consensus that has risen around *Plateosaurus* in recent years (Bonnan and Sentor 2007; Mallison 2010a, b). Christian et al. (1996) argued that the powerful adductor muscles present in *Plateosaurus* were required to counteract the abducting forces inherent in a semi-erect hindlimb. However, Mallison (2010a) has shown that, apart from placing severe constraints on the range of motion in both the neck and hindlimb, a quadrupedal posture with the limbs slightly splayed would also displace the centre of mass posterolaterally whenever the hindlimb was lifted from the ground. Instead, Mallison (2010a) argues that in order to avoid toppling, large adductor forces would have been necessary to steady the feet directly beneath the centre of mass (the pelvis) whilst walking bipedally. As *Plateosaurus* occupies a relatively basal position on the sauropodomorph tree (being the first of the truly 'large-bodied' forms) it is probable that the hindlimb in all subsequent forms was also oriented with the feet placed directly beneath the body, parallel to the sagittal midline. This scenario is supported by parsimony (being seen also in

Sauropoda) and was probably the case irrespective of the amount of bipedalism natural to each form.

The advanced understanding we now have of the range of motion and limb dynamics of *Plateosaurus* (Bonnan and Senter 2007; Remes 2008; Mallison 2010a,b,) provides something of a working paradigm when undertaking similar reconstructions of other large-bodied sauropodomorphs. *Antetonitrus* (along with most sauropodomorphs) shares with *Plateosaurus* a suite of features related to a fully erect hindlimb posture (e.g. a fully perforate acetabulum with a transversely broadened dorsal margin (= supra acetabular crest) (inferred from referred material but also observable in all non-eusauropodan sauropodomorphs); a medially oriented femoral head; and distal condyles roughly perpendicular the long-axis of the femoral shaft). Unfortunately, the incompleteness (and potential disassociation) of the *Antetonitrus* assemblage prevents full comparison with the virtual skeleton of *Plateosaurus*. However, bones that are attributed an unambiguous function (or range of motion) in *Plateosaurus* allow us to underscore and test the significance of any departures from this organisation observed in *Antetonitrus*.

There are several important differences between the hindlimb elements of *Plateosaurus* and *Antetonitrus*. While a number of these changes relate primarily to increased body size (being repeated in trends throughout both Dinosauria and Mammalia) and do not, in themselves, indicate any specific locomotory strategy in *Antetonitrus* (see Carrano 1998, 1999, 2001, 2005), taken together they presage the graviportal condition observed in Sauropoda. The principal (and most diagnostic) of these changes are: an eccentric (transversely widened) femoral shaft in which the lesser trochanter is displaced laterally and the fourth trochanter migrated disto-medially (see **Fig. 28**); a robust tibia that is reduced in length relative to the femur; and a stout, sub-plantigrade metatarsus with the main weight-bearing axis shifted medially.

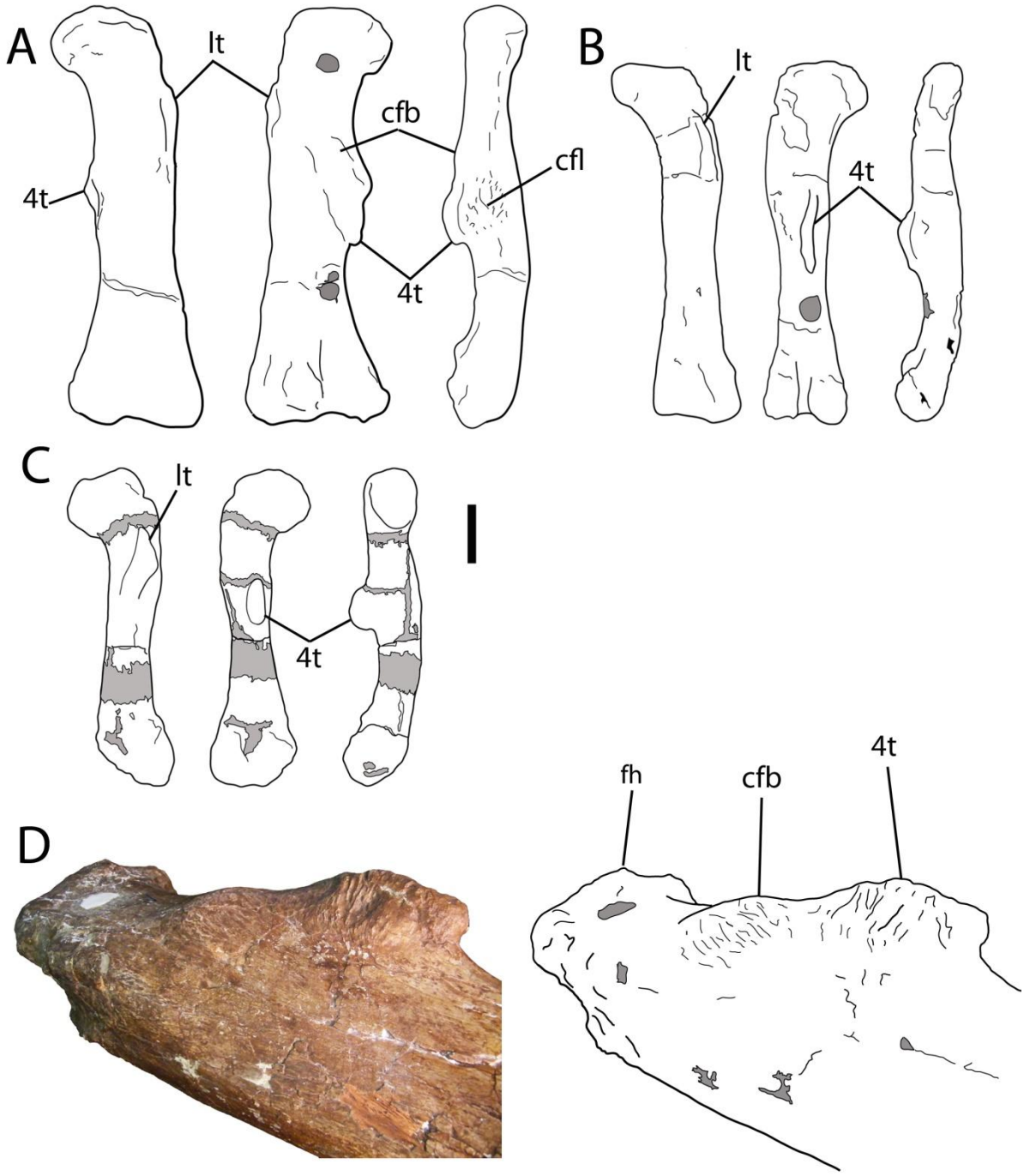

Fig. 28. **A**-**C**: Femoral variation in selected sauropodomorph taxa from the Elliot Formation of South Africa. **A**, *Antetonitrus ingenipes* (BP/1/4952) in anterior, posterior and medial view; **B**, *Aardonyx celestae* (BP/1/6510) in anterior, posterior and medial view; **C**, unnamed sauropodomorph (BP/1/4910) from the Lower Elliot Formation in anterior, posterior and medial view. Note the primitive morphology of **C**, especially the plesiomorphic position of the major trochanters. Scale bar = 10cm. **D**: Femur of *Antetonitrus ingenipes* (BP/1/4952) in posterolateral view emphasising the hypertrophied attachment cite for the M. caudofemoralis brevis. Abbreviations: 4t, fourth trochanter; cfb, M. caudofemoralis brevis insertion site; cfl, M. caudofemoralis longus insertion site; fh, femoral head; lt, lesser trochanter.

However, a notable difference between the hindlimb of *Antetonitrus* and 'true' sauropods can be observed in the major sites of muscle attachment. Due to the need to diffuse points of peak stress across a wider area of bone, along with a concurrent reduction in the flexion/extension movements of the lower limb, the osteological correlates of the musculature system are significantly reduced in fully graviportal, columnar-limbed sauropods (Wilson 2005b; Carrano 2005). In contrast, *Antetonitrus* continues to display many of the associate pits, ridges, and striations of an extensive muscular complex built to withstand large loading forces and facilitate efficient flexion/extension. One such process, the cnemial crest (attachment for Mm. femorotibialis, Mm. iliotibialis and M. ambiens), remains a pronounced, anteriorly projecting and mediolaterally expanded process as in most 'prosauropods'.

Additionally, the femur of *Antetonitrus* exhibits a prominent muscle scar posterior and slightly proximal to the plesiomorphically massive fourth trochanter (**Fig.28**). This area of bone alludes to the hyper-development of a specific muscular process that is not explicitly evident anywhere else within Sauropodomorpha. Including the fourth trochanter and its associated muscle scars, this roughened, elevated area of bone accounts for approximately 40% the total circumference of the femoral shaft at that point. Establishing the precise nature of this femoral attachment is hindered by a paucity of research into the functional myology of the sauropodomorph hindlimb (*cf*. Fechner 2009), and an in-depth investigation into its phylogenetic and/or functional significance is beyond the scope of the current project. Nonetheless, the bio-mechanics of both living and extinct archosaurs (including dinosaurs) have been covered extensively in recent years (e.g., Gatsey 1990; Carrano 1998, 2001, 2005; Hutchison and Gatsey 2000; Carrano and Hutchinson 2002; Bates and Schachner 2012; see Dilkes et al. 2012 for a helpful review), and these studies provide a basic touchstone when investigating soft-tissue structures of both avian and non-avian dinosaurs.

As mentioned above, as one approaches Sauropoda the fourth trochanter moves from a proximal position on the posterior side of the femur to a position midway down the medial edge of the femoral shaft. The fourth trochanter houses the attachment sites for the caudofemoralies group of muscles which, in representing the main femoral retractors, are recognised as the key propulsive agents during dinosaur locomotion (Gatesy 1990). It is

possible that the medial shift of the fourth trochanter in large-bodied, advanced sauropodomorphs (= sauropodiforms) represents a mechanical solution to the need to conserve traditional lines of retraction with a wider-spaced gait. In addition to its properties as a femoral retractor, Bates and Schachner (2012) have also demonstrated the ability of M. caudofemoralis brevis to adduct the femur in a number of dinosaurian taxa. However, a more medially oriented fourth trochanter, while possibly conserving the optimum line of action for the major femoral retractor (M. caudofemoralis longus), would have located the M. caudofemoralis brevis directly beneath the iliac post-acetabular process, possibly limiting the degree to which this muscle could exert adductor-forces upon the femur. Therefore, a lateral expansion of the M. caudofemoralis brevis onto the posterior side of the femoral shaft potentially represents an intensification of its adductor-based properties during hindlimb retraction. It is also possible that the medial shift of the insertion point of the M. caudofemoralis longus also represents an additional adduction mechanism, but this is harder to quantify.

The functional implications of this musculature organisation remain as speculative as the above reconstruction, however, it is unlikely that *Antetonitrus* would have required the additional power (or support) of a specialised adduction/retraction mechanism if its weight was distributed across at least three limbs at all times (i.e. while walking quadrupedally). As mentioned above, Mallison (2010a,b) has shown (in the sauropodomorph context) that large adduction forces are required in order to keep the feet positioned close to the parasagittal midline when walking bipedally. It is therefore hypothesised that the expansive process adjacent to the fourth trochanter represents an amplification of the adduction/retraction forces required to facilitate a degree of facultative bipedality in a large animal that may have also been saddled with the additional weight of a lengthened forelimb. This is further supported by the lateral shift of the lesser trochanter (insertion for Mm. Iliofemoralis group) which, in its derived position on the proximolateral corner of the femoral head, has been hypothesised as providing a counteractive abductor-moment in order to stabilise the support phase of the stride in an adducted biped (Hutchinson and Gatesy 2000; Bates and Schachner 2012). Finally, Dilkes (2000) has also observed the autopomorphic incursion of the M. caudofemoralis brevis onto the posterior surface of the femoral shaft in certain hadrosaur taxa – facultative bipeds of similarly impressive stature.

The retention (albeit rather reduced) of sub-cursorial locomotor abilities in *Antetonitrus* may have presented a considerable advantage in a Late Triassic ecosystem in which the faster predatory cursors were of considerably smaller size (e.g. *Coelophysis*), but in which large ambush predators (e.g. the 'Rausuchidae') were still active. Bipedality, in association with efficient flexion/extension motions at the elbow and knee would have also been of obvious utility during feeding (i.e. when rearing to reach high vegetation), while possibly playing an additional role in inter and intra-specific aggression displays and mating. Nonetheless, other features (including those mentioned above) of the *Antetonitrus* skeleton can be viewed in the context of a sauropod-like reduction in the range of available motion. The near-horizontal orientation of the anteroposterior axis of the proximal tibia suggests that, even with the retention of a large cnemial crest and its associated muscle attachments, the knee had begun to move towards a less-flexed, more columnar resting position. Furthermore, the shortened distal limb elements (i.e. tibia) along with the relatively distal placement of the major points of muscle insertion of the femur (i.e. the lesser and fourth trochanters) typifies a sauropod-like locomotor strategy in which power was favoured over speed (see Carrano 1999, 2001).

5.2 A BRIEF WORD ON EARLY SAUROPOD PALEOECOLOGY

The early record of the diversification and evolution of Sauropoda is extremely poorly known. Initially, the consensus view of a reciprocally monophyletic 'Prosauropoda' and Sauropoda contributed to an understanding that early sauropods were simply 'low diversity' without positing any serious hypotheses as to why this may have been the case (e.g., Barrett and Upchurch 2005; Upchurch and Barrett 2005). This can likely be seen as an extension of the 'ghost-lineage' brand of thinking that assumed a divergence point from other sauropodomorphs (i.e. the 'Prosauropoda') sometime in the Carnian without questioning the conspicuous absence of candidate sauropod ancestors for the ensuing 20+ million years (e.g. Sereno 1999; Wilson 2002). The paraphyletic 'Prosauropoda' consensus that has emerged in recent years has significantly advanced our understanding of sauropod origins, with several relatively strong candidates for the ancestral sauropod condition now known

(e.g. *Blikanasaurus*; *Lessemsaurus*; *Antetonitrus; Camelotia; Isanosaurus*). However, the relative abundance of these comparatively derived forms within the late Triassic only makes the near-absence of any sauropod-grade animals from the earliest Jurassic all the more noteworthy. This invites the question: is the paucity of information surrounding early sauropod diversification merely an artifact of inadequate sampling of Early Jurassic formations, or is there another – possibly ecological – explanation for the scarcity of sauropod-grade animals from these deposits?

Prior to the rise in sauropod abundance and diversity (as evinced by forms such as *Shunosaurus*, *Barapasaurus* and *Patagosaurus*) in the early Middle Jurassic, the only relatively well-known Jurassic-age sauropods are *Vulcanodon* from the ?Toarcian of Zimbabwe (Copper 1984; Yates et al. 2004) and the similarly aged *Tazoudasaurus* from the late Early Jurassic of Morroco (Allain and Aquesbi 2008). Earlier forms of Jurassic sauropod are possibly represented by *Gongxianosaurus* from the Ziliujing Formation of China (He et al. 1998) and the fragmentary 'Spion-Kop sauropod' from the Upper Elliot of South Africa (Yates et al. 2012). However, both of these latter taxa are still awaiting formal diagnosis and the stratigraphic and taxonomic constraints of *Gongxianosaurus* remain poorly studied. Additionally, the basal-sauropod status of *Chinshakiangosaurus* from the early Jurassic Fengjiahe Formation of China rests entirely upon a single dentary, rendering its taxonomic relationships somewhat speculative for the time being (Upchurch et al 2007a).

In contrast, a multitude of sauropodomorph dinosaurs are present in the early Jurassic that are unambiguously non-sauropodan in both taxonomy and morphology. The Hettangian to Pliensbachian mudstones and aeolian sandstones of the southern African Upper Elliot and Clarens formations preserve abundant remains of *Massospondylus* as well as the slightly larger and more derived *Aardonyx* (Cooper 1981; Yates et al. 2010). In China, the lower Lufeng formation records the massospondylid *Lufengosaurus* and the basal sauropodiforms *Yunnanosaurus* and *Jingshanosaurus* (Young 1951; Zhang and Yang 1994; Barret et al. 2005; 2007). The basal sauropodomorph assemblage of the early Jurassic North America has also risen to three valid genera recently, and now includes *Anchisaurus* from the (?Sinemurian) Portland Formation in the Hartford Basin (Galton 1976; Yates 2004; Sereno 2007; Yates 2010), *Sarahsaurus* (previously considered a specimen of *Massospondylus*) from the western (Sinemurian–?Pliensbachian) Kayenta Formation (Rowe et al. 2011), and the

recently described *Seitaad* from the overlying Navajo Sandstone unit in Utah (Sertich and Loewen 2010). In Argentina, Martinez (2009) has described multiple skeletons of a new massospondylid, *Adeopapposaurus*, from the Lower Jurassic Canon del Colorado Formation in San Juan Province and, more recently, Pol et al. (2011) named *Leonerasaurus*, a particularly gracile form from the (?Pliensbachian–Toarcian) Las Leoneras Formation of Patagonia. A basal sauropodomorph has even been described from the Early Jurassic Hanson Formation of Antarctica (Smith and Pol 2007).

The relative abundance of non-sauropodan sauropodomorphs recovered from formations dating to the earliest Jurassic, along with the near-total absence of sauropod remains, suggests a genuine palaeoecological pattern that has never been adequately scrutinized. Recently, Irmis (2010) has drawn attention to the general dinosaur-wide drop in diversity beginning at the Sinemurian, citing as a probable explanation the increasingly arid conditions in some areas that created unfavourable conditions for body-fossil preservation along with the reduction in available rock outcrop area as a result of such natural phenomena as the Drakensberg volcanics and changing sea-levels (see also Mannion et al. 2011 and refs therein). This conclusion, although not questioned here, nonetheless fails to explain the comparative paucity of sauropod-grade animals in deposits where more basal taxa are comparatively common, especially following the Late Triassic peak in diversity of the large-bodied transitional forms. Is it possible that the reduction in optimal preservation conditions noted by Irmis (2010) is indicative of an auxiliary palaeoenvironmental process – one that biased towards the preservation of non-sauropodan sauropodomorphs over their larger, more robust counterparts?

The end of the Triassic has long been regarded as a period of major environmental and ecological fluctuations (e.g., Raup and Sepkoski 1982; Benton 1991; see Sues and Fraser 2010). In the marine realm a major extinction occurred among invertebrates (Hallum 2002), and most groups of temnospondyls and crurotarsian archosaurs disappeared near or at the Triassic/Jurassic boundary (Benton 1986; Lucas and Tanner 2007). This implies a degree of ecological reorganisation that likely affected all major continental tetrapod faunas even if it did not lead to the wholesale extinction of many (e.g., Dinosauria). While the precise cause(s) of this event has eluded consensus (see Sues and Fraser 2010), the climatic repercussions are readily observable in the majority of Early Jurassic strata. In South Africa

the fluvial flood-plains of the late Triassic Lower Elliot Formation are replaced by the braided streambeds of the substantially drier Upper Elliot formation which, in turn, merge into the aeolian dunes of the Clarens Formation (Bordy et al. 2004, 2005). Similarly, the Navajo Sandstone of the south-western USA also records the dramatic rise in global aridity that appears to have marked the outset of the Jurassic (Irmis 2010).

The pervasive global distribution of these arid to near-arid conditions suggests a level of environmental drying that may have precluded the large bodied, transitional taxa from participating in most early Jurassic ecosystems. The Late Triassic deposits where these forms are found (e.g., the Lower Elliot Formation; the Los Colorados Formation) are generally characterised by the presence of thick alluvian plain sediment suggestive of a humid or sub-humid depositional environment (Anderson et al. 1998; Caselli et al., 2001; Arcucci et al., 2004; Bordy et al. 2004). In such a landscape, dominated as it would have been by low-lying marshes and riparian forests, it is not difficult to envision the amount of plant-material required to support a large bulk-browser equivalent in size to *Antetonitrus*. In comparison, the drier conditions of the early Jurassic appear to have favoured smaller, generalised feeders such as *Lufengosaurus* and the relatively gracile *Massospondylus*.

While the period of global aridity that marked the onset of the Jurassic failed to completely extinguish the sauropod-line, the fringe environment(s) (or refugia) that sustained them as a minor component of early Jurassic tetrapod communities is yet to have been properly elucidated. When conditions improved towards the end of the Early Jurassic, the adaptations that had facilitated an increase in size and a move towards graviportal locomotion in several sauropodomorph lineages at the end of the Triassic once again proved advantageous, with the sauropods ultimately displacing their more gracile cousins. Allain and Aquesbi (2008) have suggested that the Pliensbachian-Toarcian boundary marks a continental mass-extinction event (correlated with observed fluctuations the marine record, see Allain and Aquesbi [2008] and references therein) in which niches long-exploited by dinosaurian groups such as ‘prosauropods’ and coelophysids were suddenly occupied by sauropods and neoceratosaurians, respectively. However, it is suggested here that this may simply represent the bioecological replacement of the generalised herbivore/carnivore guilds by more specialised forms that were buoyed by the improved environmental circumstances of the early Middle Jurassic. The degree to which direct competition from

sauropod dinosaurs may have led to the demise of the prosauropod grade has been inconclusively speculated upon in the past (see Barrett and Upchurch 2005; Upchurch and Barret 2005). Accordingly, evidence continues to be too sparse to make any meaningful contribution here, but it appears that scenarios that posit a superior feeding apparatus in basal Sauropoda can be eliminated due to the relatively plesiomorphic morphology of the dentition is the basal sauropod taxa *Chinshakiangosaurus* and *Tazoudasaurus*. More probably, it was due to a confluence of factors centring on the acquisition of large size, a quadrupedal gait, an elongate neck, and what may have been a novel mode of in-gut food processing (see Sander et al. 2011).

The above scenario remains purely hypothetical, and its corroboration – much as its refutation – requires a considerable increase in the amount of collecting-intensive fieldwork within the pertinent sauropodomorph-bearing beds of the Lower Jurassic. Unfortunately, it may be decades before the sampling and taphonomic biases that currently obfuscate an accurate reading of the sauropodomorph record can be disentangled from genuine biogeographical and palaeoecological signals. Accordingly, Marrion et al. (2011) have recently discussed in detail the various ways in which sauropodomorph diversity patterns are strongly influenced by fluctuations in the quality of our sampling of the rock record. Nevertheless, the rate at which sauropodomorph research has expanded in the past decade is certainly promising, and the possibility that the sauropod line may have very-nearly gone extinct before it even got started certainly warrants further investigation.

6. CONCLUSION

Our understanding of the stepwise acquisition of features leading to the highly specialised bauplan of sauropods has increased dramatically over the past decade. *Antetonitrus*, for the moment being, is perhaps the best exemplar we have of the morphological halfway point on the continuum between the generalised locomotor strategy of ‘prosauropods’ and the columnar graviportalism of later sauropods. While it now appears that some large-bodied basal sauropodomorph taxa developed an obligate form of bipedality (i.e. *Plateosaurus*), others (e.g. Sauropodiformes; possibly the Riojasauridae) had begun (or continued) to utilise

the forelimb as an important additional support appendage during locomotion. This was achieved by the relative lengthening of the forelimb in association with an incipient form of manual pronation and a shortened, sturdier hand.

Nonetheless, there appears to have been a modest disjuncture in the relative speed of evolution between the fore- and hindlimb, with the forelimb maintaining a largely plesiomorphic morphology while the hindlimb acquired a number of sauropodan features relatively early in massopodan evolution. The retention of primitive features in the forelimb of *Antetonitrus* is probably related to the need to preserve the mobility of the forelimb as an important grasping apparatus, whereas the comparatively derived morphology of the hindlimb is explainable via the reorganisation of mass-reaction forces at increased body sizes. The combination of increased physical size and a (potentially) lengthened forelimb meant that *Antetonitrus* (and potentially other sauropodiform taxa) may have evolved a unique form of facultative bipedalism in order to maintain a competitive edge in an environment that rewarded the retention of modified rearing and/or cursorial abilities. In *Antetonitrus* this can be seen (speculatively) in the large muscle scar posterolateral to the fourth trochanter. This scar is hypothesised to represent the hyper-development of the M. caudofemoralis brevis. An amplification of the adductor-based powers of this muscle may have been instrumental in stabilizing the parasagittal placement of the feet beneath the body during bipedal locomotion.

Presently, our understanding of the phylogenetic interrelationships of Sauropodomorpha is derived from cladistic analyses that fail to consider the full spectrum of character data relating to functional myology and its osteological proxies. A picture is only now beginning to form of the distinct locomotor strategies practised by various elements within Sauropodomorpha, with groups such as the Plateosauridae acquiring obligate bipedalism whilst others – such as Sauropodiformes – appear to have committed to neither an exclusively bipedal nor quadrupedal posture. The future formulation of osteological characters will hopefully express our advanced understanding of these functional morphologies. An expanded matrix that takes account of such proxies will allow us to test whether the functional observations of recent studies (e.g. Remes 2008; Mallison 2010a,b; the above) provide a phylogenetic signal that may further illuminate the convoluted relationships of sauropodomorph dinosaurs.

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8. APPENDIX

8.1 OSTEOLOGICAL MEASUREMENTS FOR ANTETONITRUS

All elements BP/1/4952 unless stated otherwise.

Table A1. Selected vertebral centra.

Element	Length	Height anterior face	Width anterior face	Height posterior face	Width posterior face
Mid-posterior cervicle centrum	170	80	89	93	90
Mid-anterior dorsal centrum	122	94	98	99	105
?Mid-posterior dorsal centrum	140	119	113	138	130

Table A2. Dorsal neural arches. Abbrebiations: NS, neural spine; PRZ, prezygapophyses; POZ, postzygapophyses; HBD; height from base of arch to top of diapophyses; HYP, hyposphene; NC. Neural canal; PD, pedicles.

Element	Width	Height	Length	NS Height	NS Length	NS Width	PRZ width	POZ width	HBD	HYP height	HYP Width	NC height	PD width	PD length
Mid-anterior neural arch	203	280	192	156	97	39	102	97	129	33	34	51	96	117
Mid-posterior neural arch	257	310	190	173	107	38	99	97	105	35	38	51	117	118
Posterior-most neural arch	330	315	160	180	100	48	131	132	104	42	51	52	152	106

Table A3. Selected caudal vertebrae. Abbreviations: NA, neural arch; NS, neural spine; C, centrum; AnF, anterior face; PoF, posterior face. * = Element broken and measurement given as preserved.

Element	Height	Width	NA length	NS height	NS length	C length	AnF height	AnF width	PoF height	PoF width
?Caudosacral/anterior caudal neural arch	315	109	168	204	96	_	_	_	_	_
Anterior-most caudal (?BP/1/4952b)	190*	150*	69*	?	?	89	109*	108	124	107
Complete mid-anterior caudal (?BP/1/4952b)	224	253	137	90	52	96	98	93	93	92
Mid-caudal	245*	c.240	139	116*	c.52	103	114	103	115	97
Posterior-caudal	162	76	130	70	47	96	70	74	74	74

Table A5. Scapulae. Abbreviations: APVL, anteroposterior length ventral end; APDL, anteroposterior length dorsal end; MLSS, Minimum length scapular shaft.

Element	Length	APLV	APLD	MLSS
Largest left (BP/1/4252)	795	395	415	c.180
Smaller left (BP/1/4952c)	710	350	400 (broken)	178
Right (BP/1/4952b)	655	310	320 (broken)	140

Table A5. Forelimb.

Element	Measurement	mm
Humerus (large right)	Total length	715
	Length Deltopectoral crest	370
	Width distal condyles	230 (broken)
	Proximal width (mediolateral) head	115
	Maximum anteroposterior length proximal half	315
	Minimum width humeral shaft	92
Humerus (small right)	Total length	500
	Length Deltopectoral crest	220
	Width distal condyles	157
	Proximal width (mediolateral) head	53 (?compressed)
	Max anteroposterior length proximal half	222
	Minimum width humeral shaft	62
Ulna (large right)	Total length	420
	Maximum anteroposterior length proximal surface	167
	Maximum mediolateral width proximal surface	111
	Minimum transverse width mid-shaft	47

	Anteroposterior length midshaft	80
	Maximum transverse width distal condyles	106 (?eroded)
Ulna (small right)	Total length	360
	Maximum anteroposterior length proximal surface	144
	Maximum mediolateral width proximal surface	103
	Minimum transverse width mid-shaft	46
	Anteroposterior length midshaft	69
	Maximum transverse width distal condyles	110
Radius	Total length	370
	Anteroposterior length proximal	126
	Transverse width proximal	59
	Width midshaft	40
	Depth (anteroposterior) midshaft	62
	Anteroposterior length distal	115
	Transverse width distal	69
Metacarpal I	Total length medial/lateral	62/92
	Proximal width (mediolaterally)	109
	Proximal depth (dorsoventrally)	77
	Distal width	94
	Distal depth	50
Metacarpal II	Total length	132
	Proximal width (mediolaterally)	105
	Proximal depth (dorsoventrally)	67
	Minimum midshaft width	40
	Distal width	80
	Distal depth	43
Manual phalanx I.1	Total length dorsal/ventral	63/89
	Proximal width (mediolaterally)	70 (broken)
	Proximal depth (dorsoventrally)	68
	Distal width	75
	Distsal depth	50

Table A6. Pelvic girdle and hindlimb

Element	Measurement	mm
Ilium (NM QR1545, right)	Anteroposterior length dorsal margin	565
	Maximum mediolateral width acetabulum	130
Pubis (left)	Total length	625
	Length obturator plate	220
	Maximum thickness (anteroposterior) iliac peduncle	99

	Width of priximal end (iliac peduncle + acetabulum)	180
	Length apron	405
	Maximum transverse width pubic apron	202
	Depth (anteropostrior) distal expansion of apron	60
Femur (left)	Total Length	775
	Mediolateral width femoral head	208
	Maximum proximodistal depth femoral head	116
	Proximal end to distal margin of 4th trochanter	440
	Proximodistal length 4th trochanter	133
	Midshaft mediolateral width	142
	Midshaft anteroposterior width	94
	Transverse width of the distal end	271
Tibia (left)	Total length	510
	Anteroposterior length proximal surface	234
	Transverse width proximal	114
	Anteroposterior length distal	132
	Transverse width distal	135
	Depth (anteroposterior) midshaft	98
	Width (mediolateral) midshaft	73
Fibula (large, left)	Total length	530
	Length (anteroposterior) proximal end	156
	Width (mediolateral) proximal	48
	Minimum anteroposterior shaft length	62
	Length distal end	137
	Width distal end	64
Fibula (small, left - incomplete)	Total length	400
	Length (anteroposterior) proximal end	102
	Width (mediolateral) proximal	65
	Minimum anteroposterior shaft length	49
Pedal ungual I	Total length	159
	Width proximal surface	69
	Depth (dorsoventral)proximal surface)	71
Pedal ungual ?III	Total Length	100
	Width proximal surface	42
	Depth proximal surface	63

Table A7. Chevrons and ribs.

Element	Measurement	mm
Dorsal ribs	Total length	1040
Anterior Chevron	Length	240
Middle Chevron	Length	196
Posterior Chevron	Length	130

8.2 MODIFICATIONS TO PRE-EXISTING DATA MATRICES.

The matrix of Yates (2007a,b) provided the starting point of the current analysis, with the modifications of Yates et al. (2010), Yates (2010), Apaldetti et al. (2011) and Ezcurra (2010) employed (see Methods and Materials: 'cladistics analysis'). Characters 354-361 were taken from Smith and Pol 2007. As in the matrices listed above, the multistate characters 8, 13, 19, 23, 40, 57, 69, 92, 102, 108, 117, 121, 134, 144, 147, 149, 150, 157, 167, 170, 171, 177, 205, 207, 222, 227, 242, 251, 254, 277, 294, 299, 336, 342, 349, and 353 were kept as ordered.

Below are the changes, pertaining specifically to *Antetonitrus* and *Lessemsaurus*, made in this study and based on personal observation of the material. Although not deleted from the matrix below, it should be noted that character 184 was 'turned off' for reasons given in the text.

Any jaw/dental characters scored by Yates et al. (2010) as present/absent were rescored as unknown in the current analysis as referral of BP/1/6119 to *Antetonitrus* is based primarily on stratigraphic location and presumed affinities of the *Antetonitrus* jaw, as opposed to any over-lapping, diagnostic features shared with BP/1/4952.

Character 162 has been reconfigured to represent any invasion of the neural arch (within any of the infradiapophyseal fossae or associated areas) by pneumatic diverticulae. Character changes are as follows: *Antetonitrus*: 0 → 1; *Cetiosaurus*: 0 → 1; *Eucnemesaurus*:

0 → 1; Neosauropoda: 0 → 0&1; *Mamenchisaurus*: 0 → ?; *Omeisaurus*: 0 → ?; *Shunosaurus*: 0 → ?; *Tazoudasaurus*: 0→ 1; *Ardonyx*: 0 → 1.

Character state changes made to Antetonitrus*:*

Ch. 131: 1 → 0&1; 132: 1 → 0; 141: 0 → ?; ch. 157: 2 → 1&2; 162: 0 → 1; 178: ? → 1; 186: 0 → ?; 211: 0→ 0&1; 237: retained as '0' but character possibly inverted; 245: ? → 0; 246: ? → 0; 247: ? → 1; 248: ? → 0; 249: ? → 0; 250: ? → 0; 251: ? → 3; 255: ? → 0; 256; ? → 0; 257: ? → 0; 258: ? → 2; 261: 0→ 1; 314: ? → 0; 307: 1 → 0; 332: 0 → 1.

Character state changes made to Lessemsaurus:

Ch: 131: ? → 0; 134; 1 → ?; 135: 1 → ?; 142: 1 → ?; 154: 1→ ?; 157: 2 → 1&2; 161: 1 → 0; 164: 1→ 0; 167: 2 → 1; 225: 1 → ?; 261: ? → 1; 267: 2 → 1; 305: 0 → 1; 306: 0 → 1; 307: 0 → 1; 310: 0 → ?.

Updated Matrix:

Euparkeria
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Anchisaurus
10???00??0102?1??11????111011?010?001010?10001100111101100?10??????
01?001101?1??012110??????10?10?000?10000000101?1[12]?0111?0011???100
1001111011?10000?010?001100?000??0000000??0100?0??0?01?00?10????11[
01]0??2110010110 0??0??1101011100100201000002000[01]10103100000?11111
00010011?00101000010110100001 0[01]11101000000110111?1?01?010???10111
?0?01??0011?10100000100 11??0????1

Antetonitrus
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1]0???????????00?000001??00[12]10001010121001000???1????100?0?01100?
??0?0011??311000[01]0110?????0010?3100???1010??????0010003???00020
10010001?????????????11101111001111111101000001001111010?????????????
???1111110????[1 2]1?00?0????31?100??1

Barapasaurus
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??1?111211??????????1?1???
?00??002??100101??00201101111120121100?0[12]1001?10?11??1????????101
?00?1???????11?????????????????????????????1111013101100011111001 1??
?11110010?????????????????????1?1?1?????????1?1????????1?????????0?????
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Blikanasaurus
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Cetiosaurus
1???11?????????
??2??0011110111110
10010002O?2001?10?1020??111110201010O???[12]?????1001??00100???01111
0103110010001?????????1?????????????????????1111013?0210?0110?1?011??
1101?00???211112??0???010?111210100010010111?????????????????????????
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Chindesaurus
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Chromogisaurus
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?0???000???10????????

Coloradisaurus
?00?1002??102?111111?1??1110??011000?10??01?10?10111011100001001001?1
0100110110l?110101?????1?10010110100112??000101010001?11?001100200100
101?01100?00?001?10011000000000000000101????00?00100?001??????000010
11210011?????????????????1?????????????????0?0?131100???011?1100200110
0101110000011010000102111010000001101100??011110?00??????00011100120
001100002100211111011

Efraasia
100?1001?010??1?111?112?1110?100???00100100000??0?10??01?0??1??????1
0?000?1?????0110100??????10010010??11?011001010100001???1?1100110100
101101101000000l??001?000000000000000001100001010O0?0110000?0?010011
212000111001101012010?11000001110100010000100131000101000010000001l0
010110100001111000010110001000000110l?001?011010?0?01?1110001??00111?
00100000100O2??0???00

Eoraptor
0001?001?01010?00110001010100000100001101000O?10110010100?011000010
01???0??1?????????????????000000?0???0?0?00?10000000001?????1000000000
00?10????000??00?00???00?000??00000011??10???100??001?00??000?0100??
0?10??00100??????20?00011?000?0?0100000110100120000211??0??00?0???10
?0011?10??0?011000010110000O?1?0011110??1?0??0?????01????0?0???00?00
10000000??000?0????1?

Eucnemesaurus
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??110???0??????

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Glacialisaurus
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Gongxianosaurus
1?????0??????????12??
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???????1??0??001??0??????0?0??00000?????????????0??0?0?1?0?000?011???
2110????1?1?????????????????????????????0?100????0?????????????????
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?2?11110002000 5????????

Guaibasaurus
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1]00??1?????110????1?0????????0????110??0?1?00??0?0?000?01[1
2]1002201100100000000?10?10110000001001000010110101000?0?011111001000?0
1101?00101110000000010110000000000?1100?00??0

Herrerasaurus
00000000?0101000000000000?000100000000001000000100010101010001000011
01000000101?0000000?1000?00000000?1000000000000000000101000100000010 0
000?000010000011??0010[01]1000000200000010000010111000011001010 0?111
0??0110000000000000120000001000001101101001000001200000001000001 0???
01?0101001000010111000101100010000100001000100100101000000110001 0000
10010000000 0?0200000000

Isanosaurus
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??0??0????
???????2??10??0?????????????????2?011000?????????????????????101?0??
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???????211112??0???001?1?0??
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Jingshanosaurus
1001?002??10211111100?0?11101110110 0?102001??1?10111011100001000????
01100000101?2110010 00??1?10110010??11101100101211001????111??010????
??1???10100??0011100?1???000000000000??10??0100000000100000?0010??
11201011100??00??0011?3100100?0100010200001001310000020110010 02??110
010110?0100110100001011110101000011010 0?12011010?00??????01011110120
00100000010?4????????

Lessemsaurus
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??0?011??0
?00???101?0000011100[12]10000000111000000?????????????????????000
1???11100101 10???????0???310?????1?0??1????00100131000000?011?10001??

?1??10110?111011?10???11111?0?000001[01]?01?1???01101100l??????????1
1??12101??00??0???311?????1

Leyesaurus
?001?00?1000211??11?????1010?1101000010110l?00?101111111l?00100010[0
2]0011??????????01?10?110??1?00?10110??1010?1111010000l?1??111100200
1000111011????0??????????????????????????????????????0000?001???000????
??100???
??010???????
12000????0???0??????00??

Lufengosaurus
100???02???0211?1?11?111111111101001010110100001011101011000l0?1????
0110??0110??01010100?011010010????0111?1101101010001l?00011100200110
111?011010002001110011000000000000001001101001000000[01]10000000001
011112[01]101110011011110111310010120100010200001001311000020l101100
2101100101100001011010000102111010100001101100100l111l0?0001?11101011
10012000110000[1 2][0 1]00410111011

Mamenchisaurus
1100011 3?11120110120000000101112??00111201010101111111012110000011l2
21010000111?201?00?????2?11[0
1]000010010001111111112l113?000111012101000011000 2?1110101010020110?
011020121000001101111111110110010111111000311001001101100l1011000100
011?0?10?1?31?111013101l?001111100110001101001002111l2??0???010?011
21010?1??0??????101011111??????1101??21?2?12111102??05?1??????

Massospondylus
1001100210002111111112110111110100001011010001100110111100010001102?
01?011001011010101??10100100101101010110[01]10101100l1100?11100200
1001111011010002001110011000000000000001011101001[01]000000000000000?
01[01]011120101110011011110111210010121100000200001001310001000l101
1001001100101110001011010000102101010000001101100100111101000l111100
011100120001000002100 20?00?011

Melanorosaurus
1001?10310002111111012111010111l???10101011010110011010ll?0000001022
0110110010??200201001101110l?00111?1000110?10021100110?0101100110110
10010111?0000001??00210000000010000000?011000110010?001100????0100??
21200000110??????00?0?2100101[12]0?000102000010013100000101101000l??
??1?010110?11101111001110011101000000110110010211010100001110010111100
1?10111000011 0?301100?11

Neosauropoda
1100011311112011012000001010111[02]11101112010101011[01]11110121100[
01]10112221110010111120[01]200000102011100001201000[01]111111[02]12[
01]112[01]000011100111101001100201210101 01[01]020111[01]011020121100
002100111001111[01]100001001110003110 01[01]00111100010100000000011000
1??1?300111101310210001111100110011 10[01]10[01]00211012??0???010?111
21010?11000011111010111111011??111100210201211111021105?11???11

Neotheropoda
00[0 1]1[0 1]002[0 1]010201001100001[0 1]000000000000110000000010[0
1]100[01]01000001[01]0001[012]0100000010110000001110001000000001?000
000000000000010110011000001000 0[01]100001020000101011001000000100000
00000[12]100011000000000101000010001011000001000100012000000010?00010

01100[12]0101010130002111010100001111100001101000 1?0110001000000000
0 1]0110111110020010110000111111000?0?000001000000000001200000?1?

Omeisaurus
1100011311112011012000001010 11?2010011120101010111110101211000001122
21110010111???0?00???1???1110000 1?0?000111011111211 13??0011101200110
1011100 2?12101010110201 10?0110201211 00?021??1?1001110010 0?0111111000
3110010001 1??????0100001000110001001?3101111013101100011111001100011
1100100211012??0???010?0102101001 1?0??111?011010?11??1????1111021020
12111110 2?105????????

Ornithischia
0010000000000?0000000?000?10110001001 00?1000000100100001000000[01]00
0100100000000100000000010010[01]01[01]000000100111001110100001000000
000010100[01]0000??0100000000?00?0?00?000000000000000[12]100000000000
1000010000100111110000010000000000000000000000000000000000110112100010
001??000?000110000000100001?0101111020000000000[0 1]001110002?01?[0
1]10000011110000000000[0 1]000000000010?000????

Pantydraco
?0???0???????????[01]00?0???1??1????000100100000010?100001?00??????
??00?000?1?10??00100011?000?00?01010??0000?100101010000100 1??1100110
1010011010 1?00???1????1?????????????????????????0??11?000100001 00????
?11?1?00?????????????????????????????????????00100121100001?????????00
11??10110?00??????????1?1?000?0000000?01?001?????????????????0011100
11?000000001001?0??00000

Patagosaurus
11???
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000110020?2001010?00201?01111120121?00?021001110 0?1?0?100???0?111?00
?1100100?11?????????????????????????????1111013101000011111001100111
110010?211112??0???0011111?101000??0?????????????????????????????????
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Plateosaurus_engelhardti
1001100110102011[01]1111121111001011000010010101011001100110001100 10
0110110110110111101100010111100101101011111100101010000110011110011 0
100[01]0110110100020011100110000000000000010110100010000000010000000
0100111120001110011011110101110010020100000100001001311001020010100 0
1111100101111000011110000101100010000101111100100110101000101110001 1
000111001000001000400000011

Plateosaurus_gracilis
?00??001?0102?110111?1??1110?101??00?10?1010?0??0?10001100??10??????
???????????1?????????????0??0110?????1110010101 0?001????1100??01??
?01101101?00?001?1001100000000000000010?101000101000000100 0?00???????
?1200?11100?1011?10101010000???10?????0?00100131100102001010001111 10
01011??000011110000101 10?010000?0??0110?????????????????????0????????
?0?0????????[2 3]????????

Plateosaurus_ingens
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?[0 1]???0?0????4????????

Plateosauravus
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101?01101?00[12]0011?00110000000001000000??10??011???0??110????????0
???[23]111001110???????????????1?????????????????00100131100101?01?????
???11??10110?0000111100001011000100000011011?????0?????????????????1
1?0????0??????????4????????

Riojasaurus
1001?00??0102011?110??00111011011000?10000100?10010?001100010000011
01?0?100101?01011??????1?001000?1??101?1000101010000010??111100110100
101101101000100111001100000000000000010111010010000000110??0?010011
212101111001111111?011111011001010001020?00100131100102011010001101l0
010110010110111010110201101000000110110010011010100??011?00011100121
011000001??13????????

Ruehleia
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??10???0???
?01???101?002001??00110010000011000000?1100001?00?0?0110?????010011
112000111100?0100??0101110100???0??00???00100131100002O??11000110110
?10110?10101101000010210001O?00?01101100l?000010100?????????????????
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Saturnalia
10?????????????????????????1??1????00?100?0??????????????????10?????1
??00???0?0??0?0000?????????01000?????000010000000??????00100100
10??01101?000010000110010000000000000001000101??0??1000??0??111011
11100010102?????????????????????????????00000111[01]0220210000000100
110010010000001001[01]000101100010000000101000100100101000000100000
00010110O0?000?001000000000

Seitaad
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011?110001110011?11100101310?00?2110??0???0?????????????0?1000001??
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1???1100000010???0???0?1

Shunosaurus
1100011З?110201101200000001011?201001112010101010011010120000110111Z
101000101l?120020???1102001000001201000111111121211l2??01011?1001?1?
10010012?110000101102l?0??01?02012100O0?11?00?100111011001?111?1?000
211001100?11000?1011001?000110000??1?3101111013101100011111?01100?11
110010021111Z??0???000?01121010?01?0????110?101???11011??11111020O2?
12111?1021105????????

Silesaurus
00?0??00?0000?00100000??0?00?0?01010?????????0010??0????01?????????0
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?001000000000001010000110000000000000??100001000O0?0?0??????111?11
10000100000?????????????????????????????000001000001001000000000?010

100?0?10000110110001001000100011010000000?0000000??11?1??00??0000000?
10???000?00110000?0?

Staurikosaurus
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?00?01001?000011?000?000000000200000?1??0101011000001100?0????1?1???
??0000002001100001?0?010?00010
?000001000?1??000?0101?000000001000000001????01?????????????????????
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Tazoudasaurus
11???010??1?????????[
02]011???1???1?????????????????00?00000???0??10?11110121?1??000??00101
0??????0002??100001??00200101011020121000????????111?1?111????11????
?01?1100100??????????010?21000100?0001?310?1???03101??0?1110000002??
11??1??1??2110011100111011?0?00100001010?1111011111?011??????????
????1??10?1????51??0????

Thecodontosaurus
?0?????????????????????????1??1??1000??????0?0?0?0???000????????????1
0?0?0?1010??011000????????00?11010??????1100101010000?1??????00010101
0?1?01101?000001??00110000000000000000?1000?0101100?01000??00?010011
2110001010011000120100011000010100000101000001210000001???0?000??011?
?01010?000011110000101100010000000101100??0110101001???110001110?1?0
00??00?0????1????????

Unaysaurus
100110011010??1?111??1??1010?1011000????????????0??00????001???000??
0?10??0?10??110100??????010?10110?????011001010100000???0?1?????0?1?0
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?120000110000?????1????110????211???0??0?????????????????????????????
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?0????0??????1????????

Vulcanodon
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???2110?10?011?????????????????????????????????????310[12]?00?01111000
100111110010?11101111001001?1??20?10001?0???11?10101101110?1??11?01
0101201111102121?05?1??00?1

Yunnanosaurus
100?1002??00??10011001??1011111????00101110?00??0?11011111001000001?
01?0?00010?????????????????10000010???0???00010?21000?1???111100[0
1]10110100?011010000001100011000000000100000?0101101000000?00?0??0??
001?0??11200?11100??01??0011?2101100201000[01]020?001001310000000110
100010?110010111?00101101000010110101010000100110010?0110101000111100
10111001???11?0000110?2?0???11?